THE MORPHOLOGY AND RELATIONSHIPS OF A CROCODILIAN, *ORTHOSUCHUS STORMBERGI*, FROM THE UPPER TRIASSIC OF LESOTHO

By

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(With 44 figures and 4 tables)

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ABSTRACT

The skull, lower jaws and most of the postcranium of the type of *Orthosuchus stormbergi* Nash, 1968 were collected in 1963, by an expedition of the South African Museum, from the Upper Triassic Red Beds Formation of Lesotho. The skull and jaws of a smaller specimen, collected from the same horizon but a separate locality, are considered to be congeneric.

The cranial table is flattened, and of typical crocodilian form and sculpturing. There is a deep otic recess, and pronounced otic notch which lies open posteriorly. The quadrate and quadratojugal are strongly inclined, and the quadrate sutures with the parietal and squamosal within the superior temporal fossa. A short bony secondary palate is developed, and the pterygoids bear prominent flanges characteristic of crocodilians.

The anterior dorsal ribs are flanged on both the leading and rear margins. The coracoid, radiale and ulnare are elongated. The acetabulum is open, and the pubis excluded from the acetabular margin. The ankle joint is crocodilian in type, and a paired row of dorsal scutes, which are imbricated and sculptured, is developed over the trunk and tail.

Orthosuchus is closely related to *Notochampsa*, *Erythrochampsa* and *Protosuchus*, and probably also to *Stegomosuchus* and *Pedeticosaurus*. It is also related to *Hemiprotosuchus* though possibly less closely.

The thecodontian heritage of *Orthosuchus* can be seen in the presence of an antorbital fenestra, small basipterygoid process, and in that the quadrate has a posterior contact with the squamosal. The lower jaw includes a prearticular, and a retroarticular process is not developed.

The musculature of *Orthosuchus* probably differed little from that of living crocodiles. As in the modern group, the hind-limb and tail musculature were probably powerful, while there was a general reduction in the lower arm and hand musculature associated with great mobility of the wrist joint, and use of the elongated carpus as an extra limb segment.

The presence of a soft secondary palate, which in life extended well back to the base of the skull, suggests that *Orthosuchus* spent much of its time in water. The laterally orientated nostrils and orbits, and the relatively longer proximal limb elements, indicate that *Orthosuchus* was less well adapted to this environment than are living crocodiles.

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INTRODUCTION

In April 1963 an expedition of the South African Museum, led by Professor A. W. Crompton (now Director of the Museum of Comparative Zoology at Harvard University) collected reptilian material from the Upper Triassic Red Beds Formation of the Stormberg Series of southern Africa. It soon became clear that among this material was a nearly entire skeleton of a new type of crocodilian. Pending further preparation and more detailed study, a preliminary description was published (Nash 1968) in which the type was named *Orthosuchus stormbergi.*

A second smaller skull had also been collected from the same horizon, but from a separate locality. An analysis of this second specimen demonstrates that this material is congeneric.

This paper is mainly concerned with the detailed description of the skull and postcranial skeleton of *Orthosuchus*. The probable arrangement of the musculature of head and limbs is given, and some observations are made as to its mode of life. The position of *Orthosuchus* in relationship to both thecodontians and crocodilians is discussed.

Fig. 1. *Orthosuchus stormbergi* type skeleton (K409). Dorsal view of the skull and postcranium.

Fig. 2. *Orthosuchus stormbergi* type skeleton (K409). Ventral view of the skull and postcranium.

HISTORICAL REVIEW

Although a number of forms of Triassic age have recently been associated with the Crocodilia, there are still only a limited number which bear a direct relationship to this group. *Notochampsa* was the first of these to be described (Broom 1904). On the basis of two specimens from the same locality (Barkly East, Cape Province, South Africa) but different horizons, Broom proposed two species within this genus which he included within the crocodilian suborder Mesosuchia. *Notochampsa istedana* was collected from the Cave Sandstone of the Stormberg Series, and the second, *Notochampsa longipes*, from near the top of the underlying Red Beds. It is now generally considered that the Cave Sandstone does not represent a separate formation, but is merely a facies of the Red Beds.

Having further developed the material of *Notochampsa istedana*, Haughton (1924) redescribed the type, and questioned its crocodilian relationship. Haughton came to the conclusion that there were close resemblances between *Notochampsa istedana* and *Pedeticosaurus leviseuri* Van Hoepen, 1915 and provisionally placed the two genera in the same family, the Notochampsidae. He considered them advanced pseudosuchians having affinities with the Crocodilia.

At this time, Haughton also reconsidered the specimen described by Broom as *Notochampsa longipes*. In his opinion Broom had attached too much significance to the resemblances between the dorsal scutes of the two forms *Notochampsa istedana* and *longipes*. Haughton considered the two types quite distinct, and erected a new genus, *Erythrochampsa*, for *Notochampsa longipes*, placing this type in the Crocodilia.

Von Huene (1925) disagreed with Haughton's and Broom's interpretations and placed both *Notochampsa* and *Erythrochampsa* in the Pseudosuchia. In his view, the Pseudosuchia contained forms all of which indicate a link between this group and the crocodilians. He postulated an evolutionary sequence with the following pseudosuchians leading to the Crocodilia: *Erpetosuchus*, *Aëtosaurus*, *Stegomosuchus*, *Sphenosuchus*, and *Pedeticosaurus*. Presumably, *Notochampsa* and *Erythrochampsa* form the final link in this series.

Broom (1927) reassessed the material of *Sphenosuchus* and returned to the question of the taxonomic position of *Notochampsa* and *Erythrochampsa*. He was now quite satisfied that their generic separation was valid, but included both within the Crocodilia. Furthermore, he questioned the evolutionary sequence proposed by Von Huene. He considered *Erpetosuchus* and *Aëtosaurus* too specialized; he believed *Pedeticosaurus* to be bipedal and not related to crocodilian ancestry, and *Sphenosuchus* to be closely allied to *Pedeticosaurus*. He was of the opinion that *Stegomosuchus* might well occupy a position close to crocodilian ancestry, though the type was too imperfectly known to be sure. Broom was of the opinion that a group of pseudosuchians of a form similar to *Euparkeria* left dry ground and inhabited the marshes, developing the comparatively feeble long limbs and flattened skulls characteristic of the crocodiles.

There is now an excellent redescription of *Euparkeria* from the Lower Triassic beds of Aliwal North, South Africa, by Ewer (1965). Ewer considered *Euparkeria* as the probable direct ancestor to advanced forms like *Ornithosuchus* and *Hesperosuchus*.

In 1930 and 1931 the first North American specimens of an ancestral crocodile of Upper Triassic or basal Jurassic age were collected from the Dinosaur Canyon Sandstone of Cameron, Arizona. Barnum Brown published a preliminary notice in 1933 in which he named the type *Archaeosuchus richardsoni* and established a new family, the Archaeosuchidae. Unfortunately, the name *Archaeosuchus* was already preoccupied (*Archaeosuchus cairncrossi* Broom, 1905, a titanosuchian), and in 1934 Brown renamed this important reptile *Protosuchus richardsoni*, changing the family name to Protosuchidae.

In a revision of the classification and evolution of the Crocodilia, Mook (1934) proposed a new suborder, the Protosuchia, to contain the single genus *Protosuchus richardsoni*. No mention was made of either *Notochampsa* or *Erythrochampsa*. Mook considered that *Protosuchus* should be placed very near the line of direct ancestry of the mesosuchian crocodiles.

Subsequently Colbert & Mook (1951) redescribed *Protosuchus*, this time relating it to both *Notochampsa* and *Erythrochampsa*. They remained firmly convinced of the crocodilian nature of *Protosuchus*, but considered that the relationships of *Notochampsa* were less certain. Consequently they suggested that the family Protosuchidae be retained in preference to Notochampsidae. In their opinion, *Pedeticosaurus* was less definitely crocodilian than either *Erythrochampsa* or *Notochampsa* and should be placed among the pseudosuchians.

Other forms for which crocodilian affinity has at some time been suggested include *Platyognathus hsui* Young, 1944, from the Dark Red Beds of the Lower Lufeng Series, Yunnan Province, China. Additional material was described by Simmons in 1965. Following Young, Simmons placed *Platyognathus* in a new family of Pseudosuchia, the Platyognathidae. He believed *Platyognathus* to be a specialized form, not on the direct line of descent toward *Notochampsa* and *Erythrochampsa*. However Romer (1972*b*) was of the opinion that this species did not merit the erection of a separate family, and included *Platyognathus* within the Protosuchia.

Microchampsa scutata, also from the Lower Lufeng Series, is generally considered a protosuchian though of an essentially new type (Young 1951; Simmons 1965).

A preliminary notice of another crocodilian, probably of Upper Triassic age, from a fissure in the Carboniferous Limestone of Glamorgan, Wales, was given by Kermack (1956). A complete description of this type is still awaited.

More recently (Bonaparte 1969, 1971) *Hemiprotosuchus leali* has been described as a crocodilian closely related to *Protosuchus*. *Hemiprotosuchus* is from the upper beds of the Los Colorados Formation, La Rioja Province, Argentina.

In 1959 Reig described the skull of *Proterochampsa barrionuevoi* from the late Middle or basal Upper Triassic Ischigualasto beds of San Juan Province, Argentina. Sill reassessed this material in 1967, and agreed with Reig that it represented an early crocodilian. Sill suggested that whereas both *Notochampsa* and *Proterochampsa* strongly resemble one another, neither genus is very close to *Protosuchus*. It therefore appeared to Sill that there were two lines of crocodilian evolution during the Triassic. *Proterochampsa* could be regarded as representing an earlier and more typical line of crocodilians, and *Protosuchus* as representing an aberrant and more terrestrial group. In Sill's view, *Chasmatosaurus* probably most nearly represents the group of thecodontians from which the Crocodilia arose.

Sill proposed a new suborder, the Archaeosuchia, an unfortunate choice in view of Brown's earlier experience. This was to contain two families, the new Proterochampsidae, for the single genus *Proterochampsa*, and, provisionally, the Notochampsidae, to contain *Notochampsa* and *Erythrochampsa*. He suggested a separate suborder Protosuchia, to contain the Protosuchidae, with the sole genus *Protosuchus*, and questionably the Sphenosuchidae, with *Sphenosuchus*, *Pedeticosaurus* and *Platyognathus*.

Sill's interpretation of *Proterochampsa* was strongly criticized by Walker (1968). In his opinion the advanced crocodilian characters described by Sill are actually phytosaurian in nature. Walker's reinterpretation of the skull of *Protosuchus* indicates its close relationship to *Notochampsa* and reaffirms the position of *Protosuchus* as an ancestral crocodile.

In Walker's view *Stegomosuchus longipes* is sufficiently well known to establish its close relationship to *Protosuchus*. He has proposed grouping these forms together with *Erythrochampsa* and *Orthosuchus* in one family, the

Stegomosuchidae. Walker suggested *Cerritosaurus* Price, 1946, from the Santa Maria Formation of Brazil, as a probable ancestor, pointing out that since *Cerritosaurus* shows resemblances to *Chasmatosaurus*, both phytosaurs and crocodiles appear to converge back on *Chasmatosaurus*.

More recently Romer (1971, 1972*a*) has demonstrated a close relationship between *Cerritosaurus* and *Proterochampsa*, and two newly discovered thecodontians, *Chanaresuchus bonapartei* and *Gualosuchus reigi*. Romer regards these four types as forming a close family, the Proterochampsidae, which represents a sterile offshoot of the primitive proterosuchian stock.

Walker (1970) has suggested a major regrouping of crocodiles and closely allied forms within a proposed order Crocodylomorpha. The Stegomosuchidae is placed as the sole family in the infraorder Protosuchia of the suborder Crocodylia, which also includes the taxa Mesosuchia and Eusuchia, now ranking as infraorders. A suborder Paracrocodylia is proposed to include the infraorders Pedeticosauria, Baurusuchia and Hallopoda. The Pedeticosauria includes only the Upper Triassic family Pedeticosauridae with the genera *Pedeticosaurus*, *Sphenosuchus*, *Saltoposuchus*, *Platyognathus* and *Hesperosuchus*.

In view of this, Romer (1972*b*) has advocated retaining the Protosuchia as a suborder, but to include both ancestral forms and those others that are trending toward the crocodiles from the typical thecodontian pattern. *Protosuchus*, *Notochampsa*, *Erythrochampsa*, *Orthosuchus*, *Stegomosuchus* and questionably *Platyognathus* and *Microchampsa* are placed in the family Protosuchidae, while *Sphenosuchus*, *Hemiprotosuchus* and questionably *Pedeticosaurus* are grouped in the Sphenosuchidae.

On the other hand, Bonaparte (1971) considers that the Crocodilia as a group are too distinct for the inclusion of *Sphenosuchus*, and has suggested that the allies of *Sphenosuchus* are found in *Pseudhesperosuchus* Bonaparte, 1969 and *Hesperosuchus*. These three forms he groups in the Sphenosuchidae within the suborder Pseudosuchia.

TAXONOMIC POSITION, DIAGNOSIS AND MATERIALS UNDER CONSIDERATION

TAXONOMIC POSITION

Orthosuchus has retained from thecodontian ancestors a number of primitive features, notably the antorbital fenestra and prearticular. However, many other characters present in *Orthosuchus* are diagnostic of the Crocodilia. These are as follows:

(1) Sculpturing of the external surfaces of the bones of the skull and lower jaw.
(2) Forwardly sloping quadrate and development of an extensive otic notch.
(3) Midline fusion of the parietals.
(4) Some degree of secondary palate formation.
(5) Firm fusion of the pterygoid and quadrate with the braincase; the pterygoid bears a flange with a guide facet on its external margin for the lower jaw.

(6) Elongated coracoid, radiale and ulnare.
(7) The acetabulum is open; the pubis is excluded from the acetabulum by a forward process of the ischium.
(8) Femur without marked fourth trochanter; no development of greater trochanter.
(9) Ankle joint of crurotarsal pattern with well developed tuber on the calcaneum.
(10) External surfaces of the dorsal scutes are sculptured.

Orthosuchus is closely related to *Protosuchus*, *Notochampsa* and *Erythrochampsa*, and indeed probably also to *Pedeticosaurus*, *Stegomosuchus* and *Hemiprotosuchus*. All these forms may reasonably be included within the same family. *Pedeticosaurus* and *Stegomosuchus* are both insufficiently known to establish the family on either type. Furthermore, although the relationships of *Notochampsa* are no longer in any doubt, it seems more reasonable to retain the family Protosuchidae because of its previous general acceptance.

Protosuchia	Mook	1934
Protosuchidae	Brown	1934
Pedeticosaurus	Van Hoepen	1915
Notochampsa	Broom	1904
Stegomosuchus	Von Huene	1922
Erythrochampsa	Haughton	1924
Protosuchus	Brown	1934
Orthosuchus	Nash	1968
Hemiprotosuchus	Bonaparte	1969

Type

Orthosuchus stormbergi Nash, 1968, SAM–K409. An articulated skeleton, nearly complete.

Horizon

Upper Red Beds Formation of the Stormberg Series, Upper Triassic.

Locality

Orange River Valley in the Qacha's Nek Province, Lesotho (formerly Basutoland).

GENERIC AND SPECIFIC DIAGNOSIS

Skull bones ornamented; extensive slender preorbital region; skull table flattened; external nares separate and terminal; temporal fenestrae approximately equal in size; upper temporal fenestra large and posteriorly situated on the skull table; intertemporal area narrow, antorbital fenestra opening into a sinuous groove posteriorly; tooth count 7–8/15–18; pronounced lateral notch lies on the premaxilla/maxilla suture; two supraorbital bones on each side; frontal enters the superior temporal fenestra; midline fusion of parietals; a deep otic notch formed by the forwardly sloping quadrate and quadratojugal and overhung by the postorbital and squamosal which together form a wide upper temporal arch; quadrate fenestrated and with a posterior articulation with the squamosal; secondary palate formed from the premaxillae and maxillae, primary palate vaulted; pterygoid and quadrate fused to the braincase, the pterygoid bearing a prominent flange with external facet to guide the lower jaw on closure; lateral and median eustachian openings lying anteriorly in the basisphenoid; small basipterygoid process present. External mandibular fenestra large; prearticular well developed; the surangular forming a horizontal flange; no pronounced retroarticular process. Vertebrae amphicoelous; dorsal ribs with both an anterior and posterior flange. The coracoid elongated, the proximal expansion greater than the distal. Humerus not greatly expanded proximally, deltopectoral crest prominent; radiale and ulnare elongated, radiale longer than the metacarpals; a pisiform and two distal carpal elements present; manus small. Iliac blade forming a pointed preacetabular process; the ischium with a forward process that excludes the pubis from the acetabulum; the astragalus and calcaneum large, the calcaneum bearing a prominent tuber; four elongated metatarsals, the fifth reduced in length. A complete dorsal cuirass of paired ornamented scutes, gastralia present.

MATERIALS UNDER CONSIDERATION

SAM–K409, the type, listed above.

SAM–K4639, skull and lower jaws in articulation. This specimen was excavated from an elevation of 2 115 metres on the slopes of Majubanek Mountain facing the Kromme Spruit River. It is from the same stratigraphic level as the type specimen.

Preservation and preparation

The general condition of the type specimen, K409, is excellent though there is some distortion of parts attributable to post-mortem damage. Further, the skull fractured during excavation, and the trunk was broken in two places. The right femur was also broken. Major breaks were restored in the field. The material was X-rayed before preparation was undertaken.

All preparation has been carried out by mechanical means, and this proved a lengthy process. The vibro-tool was used extensively, but much of the work was done with the use of a pin-vice. A few areas of bone had been eroded before preservation, and these parts were restored with N.H.P. self-hardening Model Plastic.

The preserved parts of specimen K409 include the skull and both rami of the lower jaw, twenty-one presacral (three or possibly four mid-dorsals are lacking), two sacral and eight caudal vertebrae, two cervical ribs, eleven dorsal ribs and rib fragments, both scapulae, the right coracoid and part of the left coracoid; the left fore-limb, carpus and manus, the proximal carpal elements and distal portions of the right radius and ulna; the entire pelvis; both hind-limbs, the tarsus and incomplete left pes, and the right astragalus and calcaneum;

a double row of dorsal scutes covering the trunk and anterior caudal region; several gastralia.

The second specimen, K4639, is a smaller skull and articulated lower jaws partially embedded in matrix. The bone is very delicate. The block is split into two halves to expose the lateral surface of the skull. It was possible to prepare the posterior region of the skull, but anteriorly it had been crushed during preservation and work was not found to be profitable in this area.

DESCRIPTION OF *ORTHOSUCHUS*

THE SKULL

The skull of the type specimen is entire and fully prepared. It is in an excellent state of preservation, although there has been slight post mortem crushing and some consequent distortion of the cranial region. The smaller specimen, K4639, lacks the extreme tip of the snout and occiput.

External features

The skull is flattened along its length. The cranial table is broad and narrows to a slender snout with a slightly bulbous tip. The entire external skull surface is sculptured in the form of an irregular pattern of shallow pits.

The antorbital fenestra is oval in shape. It opens posteriorly into a sinuous groove which runs obliquely down towards the lateral orbital margin. The orbit is large, and is directed outward and forward. Laterally, paired supraorbitals together form a complete functional dorsal roof to the orbit. These elements are triangular in shape, the anterior supraorbital being the larger of the two. Sclerotic bones are not present. The temporal fenestrae are of approximately equal size, and they approximate the size of the orbit.

Dermal roofing elements (Fig. 3)

Premaxilla

The premaxilla meets the tip of the nasal anteriorly on the snout, and together these elements form a curved suture which passes back from the posterior border of the external naris. The posterior margin of the premaxilla lies within a deep backwardly directed notch on either side of the snout.

The premaxilla curves round to the palatal surface of the skull where it makes a small contribution to the formation of a secondary palate. At the tip of the snout, the premaxillae meet in the midline. Behind this, each borders a premaxillary foramen which lies obliquely orientated to the long axis of the skull. The medial edge of the foramen is made by the maxilla. In life the premaxillary foramina would have been closed by membrane, as in living crocodiles. The premaxilla also extends inwards as a rounded area of bone behind the premaxillary foramen, where it is sutured with the maxilla.

Each premaxilla carries four (previously described as six) discrete alveoli. Two entire teeth are known, most of the remainder of the alveoli hold broken teeth. The teeth are conical and recurved, and the crowns bear longitudinal striations. Internal to the alveolar border the premaxilla is perforated by vascular and nervous foramina.

Nasal

The nasal is a large element forming most of the dorsal surface of the rostrum. There is a distinct suture between the nasals in the midline. The tip of the snout has been superficially weathered away, but the bony bar which separates the nares must have been formed by the nasal, much as in the modern alligator, *Alligator mississippiensis*.

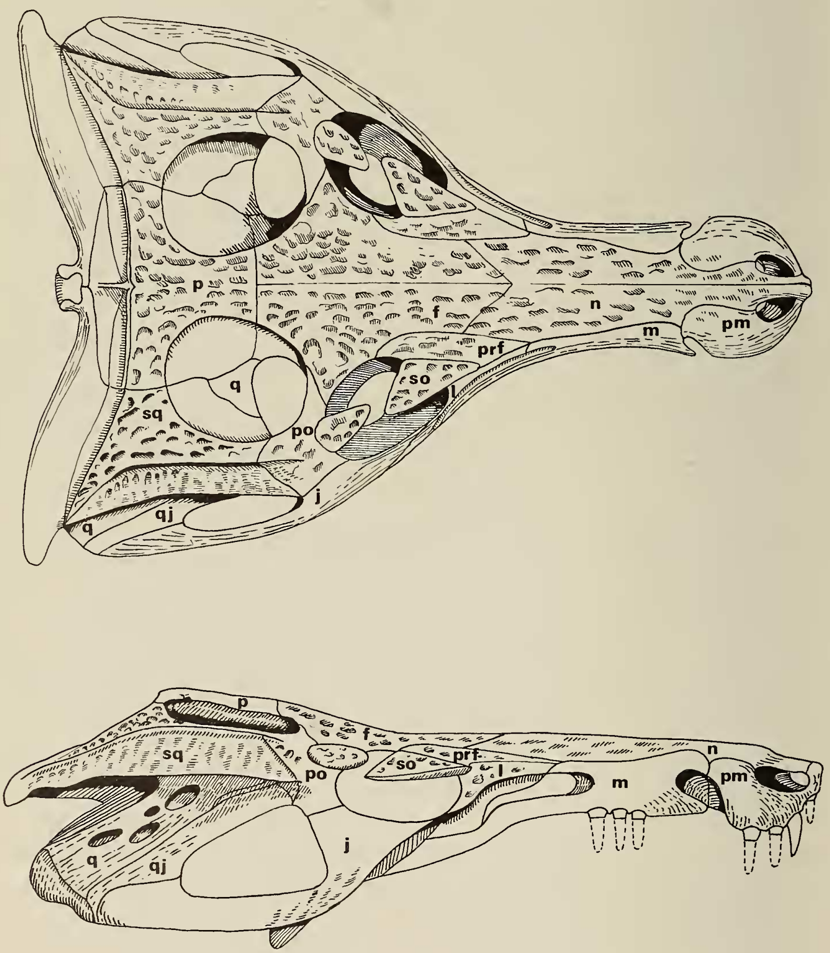

Fig. 3. *Orthosuchus stormbergi*. Reconstruction of the skull (natural size). A. Dorsal view. B. Lateral view.

The nasal unites laterally with the premaxilla and, behind the lateral notch, with the maxilla to the level of the antorbital fenestra. Posteriorly the nasal forms a wedge of bone which meets the prefrontal laterally, and the frontal medially.

Frontal

The area previously shown as the prefrontal (Nash 1968) is no longer regarded as a discrete element, but as part of the frontal. The frontal is a paired element, as it generally is in mesosuchians, e.g. *Alligatorellus* and *Goniopholis*. This is unlike the condition in the eusuchians, where both the frontals and parietals are fused in the midline.

In *Orthosuchus* an anterior process of the frontal interposes between the nasals in the midline. Laterally each frontal forms a curved suture with the prefrontal. The frontal broadens considerably and extends postero-laterally to form an oblique suture with the postorbital. A medial process extends posteriorly to meet the parietal within the margin of the superior temporal fenestra. A part of the orbital margin is formed by the frontal, as is the anterior margin of the superior temporal fenestra. The laterosphenoid makes broad sutural contact with the posterior medial process of the frontal on its ventral surface.

Parietal

This forms the greater part of a narrow temporal bar separating the two superior temporal fenestrae. In specimen K4639, a median suture is discernible, a juvenile condition, but in K409 the left and right parietals have fused together to form a single element. There is no trace of a pineal foramen.

Only the anterior third of the superior temporal fossa* is open from below for the passage of the m. adductor mandibulae externus profundus (= temporalis adductor). Laterally the quadrate and squamosal form part of the floor of the fossa, while medially the remainder is formed by the parietal. The parietal also forms the major part of the posterior wall of the fenestra, and meets the squamosal in an interdigitating suture.

The posterior edge of the parietal is concave and is bent down to form the superior edge of the occiput where it meets the supraoccipital ventrally. A small foramen, visible on the left side, probably in life provided passage for the temporal artery which ran through a canal into the superior temporal fossa. Part of the roof of this canal is formed by the parietal and part by the squamosal, while the floor is made by the supraoccipital and exoccipital.

Maxilla

Anteriorly the maxilla forms a knife-like edge which projects forwards and conceals part of the lateral notch. Behind this it forms the lateral wall of the rostrum and the anterior and lateral margins of the antorbital fenestra.

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* The terms 'temporal fenestra' and 'temporal fossa' are not synonymous. The former is used for the opening in the side of the skull; the latter refers to the space within the skull medial to (for instance) a superior temporal fenestra.

Unfortunately, the type is damaged on both sides at the anterior margin of the orbits and a suture between the maxilla and jugal cannot be seen with any certainty. However, it seems likely that the maxilla was excluded from the border of the orbit by the lachrymal and jugal. By inference, the maxilla probably excludes the jugal ventrally from the lateral margin of the post-palatine vacuity.

On the palatal surface, and at the level of the mandibular notch, the maxillae extend towards one another, meeting in the midline to form a short secondary palate. An anterior process from each maxilla runs forward between the premaxillae and the premaxillary foramina. Paired, elongate choanae open at the level of the first maxillary tooth, and extend back to the palato-maxillary suture. The alveolar wall of the maxilla borders the choana and carries three or four alveoli.

Jugal

An anterior process of the jugal forms the lateral margin of the orbit. This process also extends inwards along its length so that it forms a shelf of bone bordering the orbital region on the palatal surface of the skull. Although sutures cannot be discerned, the jugal probably forms a short suture with the lachrymal and, more posteriorly, with the maxilla on the palatal surface. Behind this, the jugal meets the ectopterygoid in a straight suture.

An ascending process of the jugal meets the postorbital to form a superficial postorbital bar. Although the postorbital bar is preserved on both sides of the skull in K409, it is traversed by numerous cracks, and no clear suturing between the jugal and postorbital is evident. The internal surface of the bar can be seen on the right side of K4639, but again there is no suture visible along its length. On balance, it seems likely that the jugal and postorbital together form an overlapping suture, as is the case in modern crocodiles. In this way the jugal reaches up to around the halfway point on the external surface of the bar, while the internal surface is formed by the postorbital.

A narrow, posterior process of the jugal forms the lateral margin of the inferior temporal fenestra. Posteriorly it forms an oblique suture with the quadratojugal.

Lachrymal

The element previously described as the lachrymal (Nash 1968) is now interpreted as consisting of both lachrymal and prefrontal. On the left side of the type the lachrymal is damaged at its extremities, and very little is preserved on the right.

The lachrymal is triangular in shape, and is sutured medially with the prefrontal. Its lateral border forms the medial wall of the antorbital fenestra and groove. The lachrymal meets the maxilla both in front of the antorbital fenestra and behind, where it forms the anterior margin of the orbit. This margin is thickened, and penetrated by a foramen which in life provided passage for the lachrymal duct.

Prefrontal

The prefrontal is bounded by the lachrymal laterally, and by the nasal and frontal medially. It forms the antero-medial margin of the orbit. Two processes of the prefrontal extend down from the internal orbital margin. The outer process lies along the internal edge of the posterior margin of the lachrymal; it is relatively short and tapers off halfway along the preorbital bar. Its extreme tip is broken so that it is impossible to be sure how far it extended, but it is doubtful that it reached the maxilla. In modern crocodiles a comparable process is found, small and never reaching the maxilla. The inner descending process passes medially and somewhat posteriorly, but again in *Orthosuchus* it is incomplete. This process corresponds to that which articulates with the pterygoid and palatine bones in living crocodiles. By inference it seems likely that in *Orthosuchus* this process met its fellow in the midline and may also have met the pterygoid ventrally.

Postorbital

This bone lies between the orbit and the temporal fenestrae and forms the anterior corner of the cranial table. Medially the postorbital unites with the postero-lateral process of the frontal in an oblique suture, while laterally it extends to form the postorbital bar with the jugal. Posteriorly the postorbital extends back a short distance between the superior and inferior temporal fenestrae to make oblique sutural contact with the squamosal. This suture lies in much the same position as it does in living crocodiles. The postorbital forms little of the lateral margin of the superior temporal fenestra, and does not contribute to its floor. Neither does it contribute to the dorsal margin of the inferior temporal fenestra.

Squamosal

This is a very large bone which forms the major area of the lateral and posterior margins of the cranial table. In K409 the borders of the superior temporal fenestra are thickened and heavily sculptured. However, in K4639 there is no such obvious thickening, a feature that again might be due to an age difference.

In the type specimen a longitudinally running groove delimits a thickened inner border of the upper temporal arch from a thinner flange which slopes down and overhangs a large, forwardly directed otic recess. In living crocodiles a groove in this position marks the junction between scales covering the skull and those covering the upper ear flap. It therefore seems probable that in life the ear of *Orthosuchus* was similarly protected by ear flaps.

In living crocodiles the ear flaps are open anteriorly when the top of the animal's head is out of water, and closed when it submerges. This action does not completely exclude water from the otic recess, but presumably it protects the tympanic membrane from mechanical injury when the animal is submerged (Shute & Bellairs 1955).

In *Orthosuchus* the otic recess is closed anteriorly by the squamosal, which extends down beneath the squamosal flange to unite with the quadratojugal below. In this way, a narrow process of the squamosal interposes between the postorbital and quadratojugal. Posteriorly the flange extends back as a tapering process, the extremity of which is carried back significantly beyond the level of the single basioccipital condyle. Posteriorly the squamosal contributes to the occiput, meeting the exoccipital ventrally and the parietal medially. Its occipital surface is not sculptured (Fig. 6).

Within the floor of the superior temporal fossa, the squamosal is sutured obliquely to the palatal wing of the quadrate, and more posteriorly forms a straight suture with the parietal. In this way the squamosal forms the external portion of the floored area of the superior temporal fossa. Anteriorly a small area of the squamosal is visible on the palatal surface, the squamosal at this point being bent very sharply back on itself. However, this is probably the result of dorso-ventral compression during preservation; this region would have been more gently rounded in life.

Quadratojugal

The anterior third of the floor of the otic recess is formed by this element, which lies with its longitudinal axis oblique to the long axis of the skull. In this way, the quadratojugal forms the posterior margin of the inferior temporal fenestra and makes an acute angle with the lower temporal arch. It is a thin, unsculptured and rather fragile element.

The quadratojugal extends back as a wedge of bone between the quadrate and the jugal. It forms an oblique suture with the quadrate, and an overlapping suture with the jugal. Anteriorly the quadratojugal meets the squamosal in a horizontal suture which runs across the internal surface of the upper temporal arch. Internally the quadratojugal is sutured to the palatal extension of the squamosal. Medially it cannot be ascertained whether the quadratojugal meets the postorbital.

Quadrate (Fig. 4)

This forms the greater part of the floor of the otic recess, and, like the quadratojugal, it is unsculptured and lies in a strongly inclined position. Its upper end meets the ventral surface of the squamosal along the lateral margin of the superior temporal fenestra to form the otic recess.

The lateral surface of the quadrate is markedly fenestrated, and dorsal contact with the squamosal is made by slender bars of bone. In recent crocodilians the tympanic cavity is linked to air passages within the quadrate and supraoccipital, and by an elaborate system of cavities and tubes to the throat.

The posterior quadrate contact in *Orthosuchus* forms a somewhat expanded head, socketed immediately beneath the rear end of the squamosal in typical archosaurian fashion. The posterior margin of the quadrate within the otic recess is curved, forming a distinct otic notch. This, together with the overhanging tip of the squamosal and paroccipital process, forms the bony housing for the tympanic membrane (Fig. 4). The posterior quadrate contact is lost in recent crocodiles, and indeed is also absent in teleosaurs such as *Pelagosaurus.*

In living crocodiles the squamosal, together with the opisthotic, extends down to gain contact with the rear margin of the quadrate, so closing the notch posteriorly. This can be seen in crocodilians of Upper Cretaceous age such as *Leidyosuchus.* The closure of the otic notch in these forms has meant that the tympanic membrane now adheres to bone all along its periphery.

Although the exoccipital in *Orthosuchus* is incomplete, it clearly overlaps the major portion of the posterior margin of the quadrate. These two bones are closely apposed, and the exoccipital blocks the major part of the primitive area of the cranioquadrate passage.

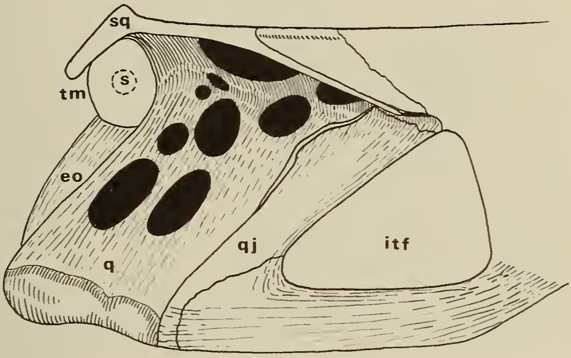

Fig. 4. *Orthosuchus stormbergi.* Reconstruction of the right quadrate of the skull, seen in postero-lateral view. The lateral flange of the squamosal has been removed to show the otic notch and suggested position of the tympanum (× 1½).

The palatal process of the quadrate passes forward and curves around the anterior margin of the floored part of the superior temporal fossa. In this way the quadrate forms a saddle-shaped area wedged in between parietal and squamosal dorsally within the superior temporal fossa. Internally, the palatal wing, as seen on the right side of the type specimen, meets the laterosphenoid in a short suture which runs vertically down from the superior temporal fossa. A semi-lunar foramen lies on this suture, and this no doubt gave passage to the three divisions of the trigeminal nerve. Below the foramen, the quadrate is sutured to the pterygoid, the suture continuing its vertical passage down to the basicranium. The quadrato-pterygoid suture then runs back for a short distance parallel to the midline before running obliquely out to the medial edge of the condylar surface. The articular surface for the lower jaw consists of two condyles separated by a shallow groove. The internal condyle is the larger of the two.

The quadrate is certainly firmly fused to the pterygoid and doubtless to the prootic also. Unfortunately, very little of the medial end of the quadrate can be made out, and it is in a poor state of preservation.

Pterygoid (Fig. 5)

The pterygoid is an extensive element. It probably reaches forward to the choanae, and extends far back to the occiput. It forms a narrow plate of bone on the floor of the basicranium where the pterygoids meet in the midline. Posteriorly the pterygoids diverge to form a narrow wing on each side which passes back to unite with the exoccipital. Medially the pterygoid wing overlaps the basisphenoid, forming a curved suture. Laterally the pterygoid is sutured to the palatal wing of the quadrate.

The quadrate ramus of the pterygoid extends vertically over the anterior wall of the braincase, as in all crocodiles. Dorsally this ramus unites with the laterosphenoid at the level of the foramen for the trigeminal nerve. Below the quadrate ramus, the pterygoid extends in a latero-posterior direction as a prominent pterygoid flange which forms an overlapping suture with the ectopterygoid. The outer edge of the flange is made by the ectopterygoid ventrally and by the pterygoid dorsally, much as in *Gavialis*. The pterygoid flange lies farther forward in *Orthosuchus*, and although it is somewhat inclined ventrally it does not descend as steeply as it does in living crocodiles. Each flange bears a facet which guides the lower jaw on closure.

The rear edge of the pterygoid flange of *Orthosuchus* is considerably thickened to form a horizontal ridge. Medially the ridge divides to run in both directions along the basicranium parallel to the midline. In addition, the pterygoids form a continuous median ridge which runs forwards from the pterygoid-basisphenoid suture to become confluent with the vomerine septum.

Immediately in front of the pterygoid flange, a triangular-shaped plate of bone extends forwards on each side to the level of the antorbital fenestra. The exact contribution of pterygoid and palatine to this area is problematical since the bone is poorly preserved. It seems likely that the pterygo-palatine suture runs transversely just in front of the pterygoid flange, the pterygoid extending forwards in the midline to meet the vomer. However, there is no possibility of verifying the presence or absence of this suture.

Ectopterygoid

This element meets the lateral edge of the pterygoid flange and then extends laterally as a flat bar of bone. Externally it meets the jugal, and may well also unite with an internal extension of the postorbital. It is unlikely that the ectopterygoid has any sutural contact with the maxilla as it has in modern crocodiles. The anterior margin of the ectopterygoid forms the major part of the posterior border of the post-palatine fenestra. Its posterior margin forms the outer half of the anterior border of the pterygoid fossa.

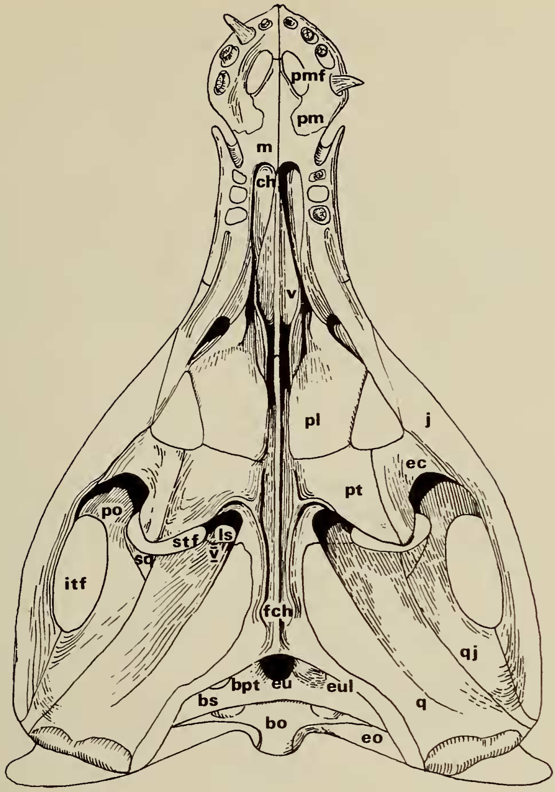

Fig. 5. *Orthosuchus stormbergi*. Reconstruction of the palate (natural size).

Palate (Fig. 5)

The type specimen of *Orthosuchus* is unique among the protosuchians in that the palate is well preserved. Although sutures are not entirely clear, there is little doubt as to the extent of the various elements. Elongate choanae open behind a short secondary palate made by the premaxillae and maxillae. The choanae correspond to what Huxley (1877) called ‘the primitive posterior nares of the Crocodilia’. In modern crocodiles these lie between the septum formed by the vomers and the anterior processes of the pterygoids centrally, the palatines behind and the maxillae in front and at the sides, and this is exactly the case in *Orthosuchus*.

In *Orthosuchus* the median septum formed by the vomers is continuous with a median pterygoid septum which runs to the rear of the skull. Laterally, each vomer forms a deep channel which opens on to the pterygoid. In this way the bony secondary palate opens into a pair of narial tubes formed by the vomers anteriorly and the pterygoids posteriorly. *Orthosuchus* differs from living crocodiles in that these tubes are not floored by bone, though there can be little doubt that they were covered by membrane in life. Hence the functional choana opened on the rear margin of the pterygoid in much the same position as in recent crocodiles.

The shape of the palatine is also suggestive of its incipient inclusion in the formation of the secondary palate. Anteriorly the palatine forms an oblique suture with the maxilla, posterior to the alveolar border. Behind this the palatine twists along its length and its lateral border appears to be in the process of rotating ventro-medially to attain the tubular shape that characterizes this element in living crocodiles.

Occiput and braincase (Fig. 6)

The occiput of the type specimen is distorted because of the dorso-ventral compression that has occurred in this region, and it would have been more nearly vertical in the natural state. Telescoping of the right quadrate, together with reduction in height of the foramen magnum, indicates the degree of compression that has occurred.

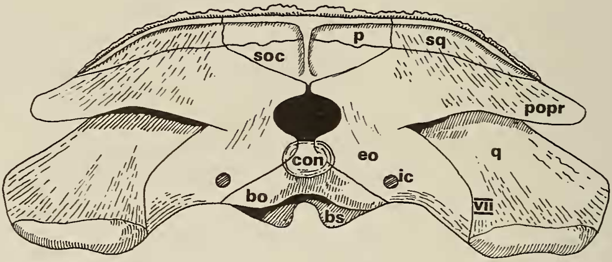

Fig. 6. *Orthosuchus stormbergi*. Reconstruction of the occiput (natural size).

Supraoccipital

This is an unpaired, triangular-shaped element which bears a median vertical ridge. It meets the parietals above in a horizontally running suture, and the exoccipitals below in an oblique suture. There is no evidence of a dermo-supraoccipital bone.

Exoccipital

The exoccipital forms the superior margin and lateral boundary of the foramen magnum, and also a small part of the occipital condyle, as in modern crocodiles. On either side, the exoccipital fuses with the large paroccipital wing of the opisthotic and divides laterally into two processes, as it does in the teleosaur *Pelagosaurus*. The more extensive upper wing is sutured dorsally to the squamosal, and the lower wing overlaps the posterior margin of the quadrate. The main trunk of the facial nerve, the ceratohyal, the orbitotemporal artery and the lateral head vein would then have passed back from the middle ear region, probably along the grooved exoccipital-quadrate suture. In living crocodiles this groove is no longer open, but is transformed into a narrow canal by the much broader fusion of the quadrate with the upper paroccipital wing.

Ventrally the exoccipital unites with the basioccipital medially, and more laterally with the pterygoid. Although the exoccipital has suffered some damage, there appears to be evidence of a small foramen lying dorsal to the exoccipital-pterygoid suture. This probably provided passage for the internal carotid artery and may also have transmitted the vagus and hypoglossal nerves. In living crocodilians twin foramina lie to either side of the foramen magnum. The inner carries the hypoglossal nerve, while the glossopharyngeal, vagus and accessory nerves and vein pass through the larger vagus foramen. Antero-ventrally to this lies a foramen through which the internal carotid enters the middle ear.

Basioccipital

Although the major part of the occipital condyle is formed by the basioccipital, this element forms only a small median part of the ventral border of the foramen magnum. The remainder of the margin is made by the exoccipital. The condyle is clearly delimited and is oval in shape. Laterally the basioccipital meets the exoccipital, and although this suture is difficult to discern, it must run downwards and outwards to the lower boundary of the rear margin of the skull. The basioccipital continues forwards on the ventral surface of the skull for only a very short distance before uniting with the basisphenoid in a curved suture. In this region there is a small basal tuber on either side for the ventral neck muscles.

Basisphenoid

The basisphenoid is seen as a half-moon-shaped element interposed between the basioccipital and the pterygoids, although very probably it extends far forwards above the pterygoids. Small basipterygoid processes lie behind the basisphenoid-pterygoid suture. A very deep pit is located in the midline and paired slit-like foramina can be seen lateral to each basipterygoid process. These foramina lie within the basisphenoid, although the anterior margin of each is formed by the pterygoid. There can be little doubt that they are the openings of the eustachian system, although no connection between median and lateral pits can be discerned. Within the median pit a narrow channel runs forwards above the pterygoid, and a larger channel runs back into the body of the basisphenoid.

Living crocodiles have both lateral and a large median eustachian opening, but they lie between the basisphenoid and basioccipital. They lead upward by a complex system of tubes to the ear, and downward by three membranous tubes to the throat, eventually forming one tube which opens almost at the level of the choanae.

Laterosphenoid

As seen on the right side of the type specimen, the laterosphenoid has the same form and relationship to other elements as found in living crocodilians.

Antero-dorsally the laterosphenoid articulates with the internal surface of the frontal, and also extends laterally and probably just touches the postorbital. Postero-dorsally the laterosphenoid unites with the internal surface of the parietal. The laterosphenoid-quadrate suture runs perpendicularly down to the foramen which transmitted the trigeminal nerve. Ventrally the laterosphenoid meets the quadrate ramus of the pterygoid.

Otic region

Nothing can be said of either the prootic or epiotic, since these elements are concealed by the quadrate, parietal and supraoccipital. The opisthotic forms the large, horizontally directed paroccipital process to which the exoccipital is fused. Medially it fuses with the supraoccipital and dorsally it is sutured to the squamosal. Internal to the quadrate, fragments of bone can be seen and very probably the otic elements were crushed during preservation due to compression of the skull in this region. The stapes is also unknown.

THE LOWER JAW (Fig. 7)

Both mandibular rami of the type specimen are well preserved although slightly distorted. The middle area of the right has been restored, and the articular region is firmly attached to the condylar surface of the quadrate. The articular region of the left ramus is incompletely preserved. In K4639, the rear halves of both rami are visible although the posterior margin is incomplete in both cases.

Dentary

This is the largest of the lower jaw elements and externally forms the lower half of the mandible. It is sculptured in the form of numerous small, shallow pits which grade into slit-like markings, more sparsely arranged, farther back. A

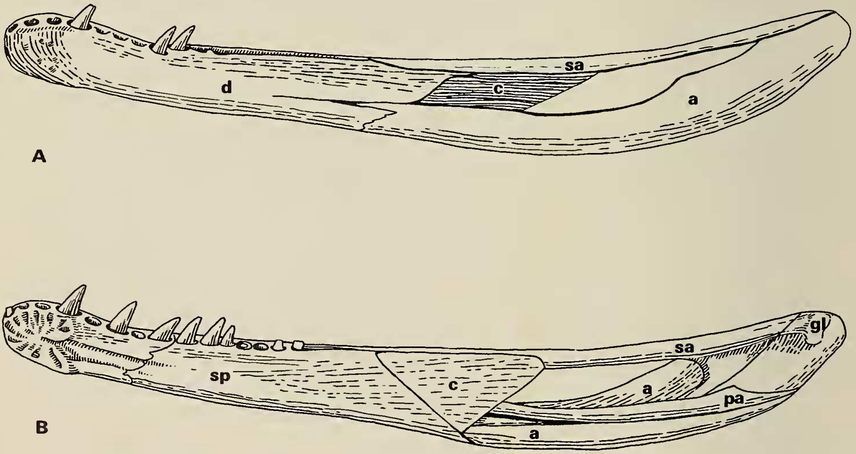

Fig. 7. *Orthosuchus stormbergi*. Reconstruction of the lower jaw (natural size). A. Lateral view. B. Medial view.

careful comparison of the alveolar border of both rami suggests that there were probably 15 dentary teeth, though up to 18 could have been present. The teeth, like those of the upper jaw, are conical, longitudinally striated and somewhat recurved. There is no differentiation of tooth shape and there appear to be no marked differences in tooth size, apart from those reflecting the pattern of tooth replacement.

The mandibular symphysis is short and stout, and is complete at the level of the fourth mandibular tooth. Extending back from the middle of the symphysis is a longitudinally running groove, the Meckelian canal. This carried the mandibular artery, vein and nerves, and was almost certainly covered by the splenial in life. This latter element may have entered the symphysis; on both rami the anterior border of the splenial is incomplete. Posteriorly the dentary extends to the anterior margin of a large, elongate external fenestra which lies between the dentary, angular and surangular.

Splenial

This element lies wholly on the anterior inner surface of the mandible, uniting with the dentary above and below. The exact position of its posterior margin is uncertain, as suture lines are difficult to distinguish in this region. Probably the splenial extended back to the mid-region of the ramus, where it united with the coronoid and, below this, to a smaller extent with the angular.

Coronoid

The single coronoid element forms the anterior margin of an extensive adductor fossa, and occupies much the same position as it does in recent crocodiles. Posteriorly the coronoid has a rounded edge which overlaps the surangular. The suture between these elements then runs forwards just below the dorsal margin of the ramus on its internal surface.

Surangular

The surangular extends over the external mandibular fenestra as a narrow flange, and in this respect the element differs from that of living crocodiles. Externally the posterior region of the surangular forms an overlapping suture with the angular. Internally it borders the adductor fossa dorsally, and behind this a descending process meets the prearticular ventrally. Posteriorly the surangular is overlapped medially by the articular.

Angular

This is a large postero-ventral element which forms the ventral border of the external mandibular fenestra. The angular wraps round the rear margin of the mandible, and is sutured internally to the articular. A retroarticular process is not developed. On the inner surface, the upper margin of the angular is bordered by the prearticular. These two elements diverge anteriorly to form a slit-like foramen, of which the anterior boundary is formed by the coronoid. This corresponds to the Meckelian foramen which, in living crocodilians, lies between the angular and splenial.

Prearticular

This element is not normally found in crocodilians, but it occurs in early mesosuchians such as *Pelagosaurus* and *Metriorhynchus*. In *Orthosuchus* it is a slender, elongate element which forms the ventral margin of the adductor fossa. Anteriorly it is overlapped by the coronoid, and may have extended forward medially to this element to contribute to the inner wall of the Meckelian canal. The foramen which transmits the chorda tympani branch of the facial nerve, and which is almost universally present on the inner surface of the prearticular, cannot be discerned. However, there is a groove running along its inner surface. Posteriorly the prearticular lies over the anterior edge of the articular.

Articular

On the right side this element is fused by matrix to the condylar surface of the quadrate, while only fragments of the left articular are preserved. The glenoid fossa cannot be seen, although from the contour of the articular area it appears to consist of a large internal and smaller external articular surfaces.

THE VERTEBRAL COLUMN AND RIBS

General features

The presacral series is complete but for a gap which corresponds to three mid-dorsal vertebrae, giving a presacral count of 24. Of these, probably eight may be regarded as cervicals. Two sacral vertebrae are in articulation with the most anterior caudal vertebra. Seven other caudal vertebrae are known, of which only one is in a reasonable state of preservation.

The vertebral column shows regional differentiation both in the progressive

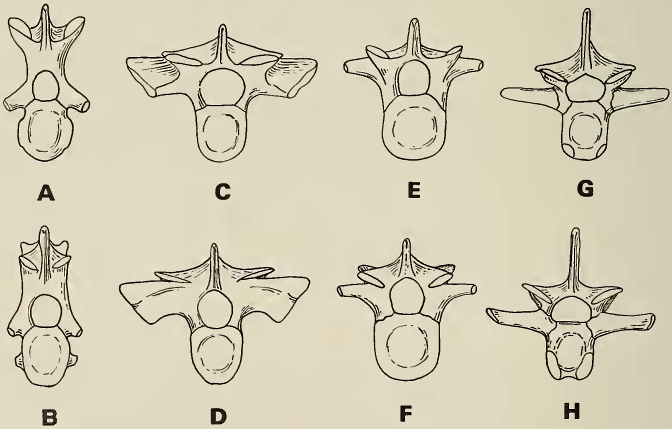

Fig. 8. *Orthosuchus stormbergi*. Anterior (upper row), and posterior (lower row) views of vertebrae (natural size). A. Cervical six. B. Cervical five. C & D. Dorsal seventeen. E & F. Dorsal twenty-four. G & H. Caudal four.

changes that occur in the rib articulation facets, and in the overall dimensions of the vertebrae. The centra of the anterior cervicals are short, and a progressive increase in length occurs through to the lumbar region, as shown in Table 1.

The vertebrae are spool-shaped and, unlike the procoelous vertebrae of eusuchians, in *Orthosuchus* they are all amphicoelous. In the majority of the vertebrae a clear sutural union of the neural arch on the centrum is visible. The neural spines are not high in any region of the column, but are tallest in the cervical region and decrease slightly through to the lumbar region. The articular surfaces of the zygapophyses are more or less vertical on the cervicals, but in the mid-dorsals they change to a more nearly horizontal direction. Posterior to this they again become more nearly vertical in orientation (Fig. 8).

Table 1

Measurements of the vertebrae in mm

Length of centrum (L). Height of centrum posteriorly (H). Width across posterior end of centrum (W). Height of neural spine (NH). Maximum height of vertebra (VH).

Vertebra No.	L	H	W	NH	VH
Cervical					
Atlas . .	—	—	—	—	15,5
Axis . . .	7,7	7,9	5,5	8,0	17,0
3 . . .	6,4	8,5	6,0	—	—
4 . . .	6,6	8,5	6,0	8,0	21,0
5 . . .	6,8	7,7	6,0	8,0	21,0
6 . . .	6,8	—	—	6,0	20,0
7 . . .	6,8	7,6	6,0	6,0	19,0
8 . . .	6,8	—	6,5	6,0	18,0
Dorsal					
9 . . .	7,4	6,5	6,5	6,0	18,0
10 . . .	8,4	—	—	6,0	18,0
11 . . .	8,4	—	—	6,0	18,0
12 . . .	8,8	7,3	6,5	6,0	18,0
13 . . .	8,8	7,3	6,0	6,0	18,0
14 . . .	—	—	—	—	—
15 . . .	—	—	—	—	—
16 . . .	—	—	—	—	—
17 . . .	10,0	7,0	6,5	6,0	18,0
18 . . .	10,0	7,5	6,5	6,0	18,0
19 . . .	10,5	7,5	6,5	6,0	18,0
20 . . .	10,5	7,5	6,0	6,0	18,0
21 . . .	10,0	8,0	6,7	5,0	19,0
22 . . .	9,6	8,5	—	5,0	19,5
23 . . .	9,6	8,5	7,0	5,0	20,0
24 . . .	9,6	8,5	8,7	5,0	18,5
Sacral					
1 . . .	10,0	8,5	7,5	7,0	18,0
2 . . .	10,0	8,0	7,0	7,0	18,0
Caudal					
1 . . .	8,0	7,0	6,2	—	19,0
2 . . .	7,7	7,0	6,4	—	—
3 . . .	7,7	7,5	6,0	9,0	20,0
4 . . .	7,7	—	6,0	9,0	20,0
Mid-caudal . (isolated vertebra)	9,0	5,5	4,5	—	—

Atlas and axis (Fig. 9)

The intercentrum of the atlas is well developed, and in cross-section forms a dumb-bell shape. A single-headed rib is in articulation with the intercentrum postero-laterally, while dorso-laterally the intercentrum supports the stout base of the pedicel of the neural half-arch on each side. Dorsally a narrow gap separates the two neural half-arches. Presumably this gap was filled by cartilage and overlapped by a pro-atlas in life, as in recent forms. Posteriorly the dorsal portion of the neural arch is drawn back to form an almost horizontal postzygapophysis which overlaps the axis. The prezygapophysis of the axis with which it articulates is not visible, but is probably quite small.

The centrum of the atlas, the odontoid process, can be seen lying between the pedicel bases of the neural half-arches of the atlas. The anterior face of this process articulates with the occipital condyle, as in living crocodiles. The postero-lateral margin of the odontoid process together with the adjacent edge of the axis centrum bears an articular facet for the second rib. This rib is closely apposed to the first, and is also single-headed.

The axis centrum is very stout, and posteriorly is pulled down to form a hypapophysis. The neural spine is long and low, and is pointed anteriorly where it projects between the atlas neural half-arches.

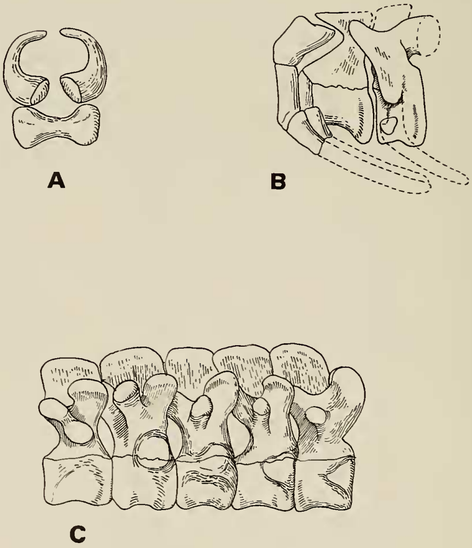

Fig. 9. *Orthosuchus stormbergi.* Vertebrae (natural size). A. Atlas seen in anterior view. B. Atlas, axis and third cervical seen from the left side. C. Anterior presacrals, vertebrae eight to twelve inclusive, seen from the right side.

Cervical vertebrae 3 to 8

The most anterior vertebrae are strongly keeled and the centrum of each bears both an anterior and a posterior hypapophysis. The keeling becomes progressively less marked through to the posterior cervicals, and is absent on vertebra eight. In modern crocodiles this keeling is extended to the anterior dorsal vertebrae, and all bear a hypapophysis.

Laterally each centrum bears a prominent parapophysis for the articulation of the capitulum. Each parapophysis is broad anteriorly and tapers to the mid-region of the centrum. On the third vertebra, the parapophysis lies near to the ventral surface, but through the succeeding vertebrae it gradually alters its position so that on vertebra eight it is borne near to the neurocentral suture.

The neural arch has a pronounced diapophysis on each side for the tuberculum. The position and shape of the diapophysis also changes progressively along the length of the cervical vertebrae. On the third the diapophysis is a thickened ridge along the anterior half of the neurocentral suture. Through the cervical series this becomes progressively raised on a transverse process.

Dorsal vertebrae (Fig. 9)

The progressive changes of the positions of the articular facets for the ribs which occur along the cervical series continue through the anterior dorsal vertebrae. The parapophysis continues to move dorsally up the anterior margin of the centrum, coming to lie beneath the diapophysis on vertebra twelve. Coupled with this movement, the parapophysis also becomes larger and more round in shape. The diapophysis does not alter its position from that seen on the eighth cervical, though both the transverse process and the diapophysis become progressively broader through to the twelfth vertebra.

Behind this the parapophysis continues to migrate upward, coming to lie on the same level, although still separate from the diapophysis on vertebra twenty-two. Both the facets and the transverse processes then diminish in size towards the pelvis so that on the last presacral the transverse process is quite slender and short and the two facets fused. In modern crocodiles these facets are confluent and the dorsal ribs single-headed on the eighteenth vertebra. In this way the transverse processes become narrower earlier on in the series.

Sacral vertebrae (Fig. 10)

The centra of the sacrals are long, slightly exceeding the length of the posterior dorsals. The transverse process of the first sacral vertebra is stout and short, as is the first sacral rib. In addition to its articulation with the transverse process, the rib also unites with the centra of both the last presacral and first sacral vertebrae. An identical condition is found in living crocodilians. The transverse process of the second sacral vertebra faces somewhat posteriorly. Distally it articulates with a very broad rib, which, as in modern crocodiles, also articulates with the posterior portion of the lateral surface of the centrum.

The sacral ribs form a very strong support for the ilium. The articular areas are triangular in shape in both cases, though that between the second sacral rib and the ilium is the more extensive. Only a very small median portion of the ilium is free.

Caudal vertebrae

Only eight caudal vertebrae are known. One of these is in articulation with the sacral series, and three others are from the proximal region of the tail. The remainder have small, elongate centra and must be mid-caudal vertebrae. Probably the tail was long, of the order of 30 to 40 vertebrae.

The neural spines of the anterior caudals are taller than elsewhere in the column, and are directed slightly backwards. The zygapophyses slope so that their facets meet more or less vertically. The first chevrons probably lie between the third and fourth caudal vertebrae. The fourth bears a nearly entire caudal rib, although elsewhere these are broken above their bases.

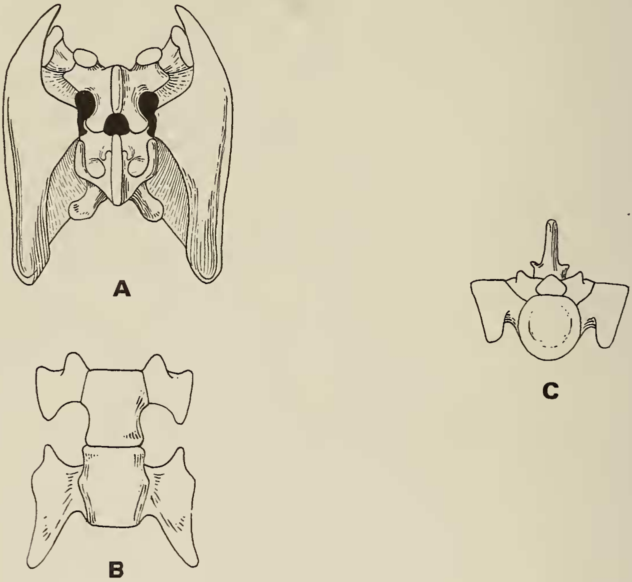

Fig. 10. *Orthosuchus stormbergi*. Sacrum, corrected for distortion (natural size). A. Dorsal view with sacral ribs and internal surfaces of the ilia. B. Ventral view with sacral ribs. C. First sacral vertebra seen in anterior view.

Ribs (Fig. 11)

The proximal ends of the atlantal and second rib are present on both sides. They are slender and single-headed. The first has a large articular facet for union with the intercentrum of the atlas, and the second rib has a smaller facet for union partly with the odontoid and partly with the centrum of the axis. This differs from modern crocodiles where the axial rib is double-headed, the second facet lying on the odontoid.

Only one other cervical rib is complete, the fifth, and this is indistinguishable in type from that of living crocodiles. It is double-headed and has a short shaft which runs parallel to the long axis of the vertebral column. The capitular and tubercular processes rise at right angles to the shaft of the rib and diverge as they pass upward to the centrum of the vertebra.

The shaft of the eighth cervical rib is transitional in type between that of the cervicals and anterior dorsals. It more closely resembles that of the latter though it is much more slender.

Behind this, on the left side, dorsal ribs nine to fourteen inclusive are preserved *in situ*. Three right dorsal ribs were also associated with the material. All the dorsal ribs are double-headed and their shafts long and strongly curved. The articular facets for the union of rib with vertebra move further apart passing from the sixth cervical back to vertebra nine, and are at their widest on this vertebra. Posterior to this they come closer together. Further, in each case, the tubercular process lies above and anterior to the capitulum, the two being separated by a shallow groove. In the ninth rib, the tubercular process is the larger of the two, but from the twelfth this is altered and the rib articulates principally by the capitular process.

Ribs nine to fourteen are expanded to form prominent antero-ventral and postero-dorsal flanges. Because of this, the mid-dorsal ribs particularly are very flat and broad proximally, and narrow abruptly to a cylindrical shaft.

The antero-ventral flange rises immediately behind the head of the rib much as in living crocodiles. In recent genera, the flange is limited to the first two to four dorsal ribs, the number being greater in older individuals. The postero-dorsal flange is more gently rounded in shape and is developed slightly lower down the shaft of the rib. Presumably this flange is homologous with the cartilaginous 'uncinate' process which is developed in this position in living crocodiles. This process is normally carried on the third to fifth dorsal ribs, and may occasionally ossify slightly. Both anterior and posterior flanges serve for muscle attachment. In *Orthosuchus* the postero-dorsal flange of one rib overlaps the antero-ventral flange of the succeeding rib.

Posteriorly only the proximal part of ribs in articulation on the left side of vertebrae eighteen and nineteen are known. These ribs are double-headed, but, unlike that of the anterior dorsals, the capitular and tubercular processes lie on the same level. The capitular process is the larger of the two. Each rib is strongly curved backwards, and is broad and flat immediately behind its head. The rib rapidly contracts to a cylindrical shaft and there is no evidence of either an anterior or a posterior flange. Probably at least the last two presacral vertebrae did not bear ribs.

Overlying vertebrae nineteen and twenty on the right side is an accumulation of the remains of several fine gastralia.

THE LIMB GIRDLES AND LIMBS

Pectoral girdle (Fig. 12)

The shoulder girdle shows a remarkable approach towards that seen in recent crocodiles. It consists of scapula and coracoid only. Both scapulae are preserved entire, although the right has been somewhat flattened during preservation. Of the coracoids, the right is fractured and its distal margin incomplete, while only the proximal end of the left coracoid is present.

The scapula is a tall element, with its superior end considerably expanded

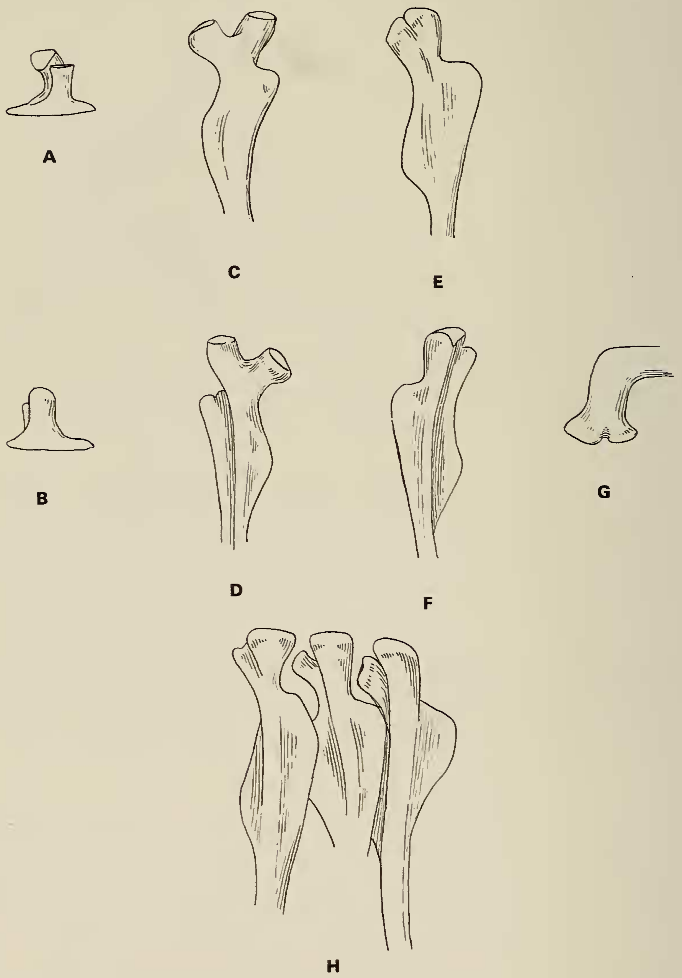

Fig. 11. *Orthosuchus stormbergi.* Lateral (upper row), and medial (middle and lower rows) views of ribs (natural size). A & B. Right fifth cervical. C & D. Right first dorsal. E & F. Right mid-dorsal. G. Left tenth dorsal. H. Left mid-dorsals showing overlapping of the rib flanges.

and drawn out posteriorly. It narrows to a stout shaft which curves sharply inwards to form a more conservatively expanded inferior region. Characteristically, the posterior margin of this bears a large rough facet which forms the upper half of the glenoid surface. Another triangular-shaped facet for the coracoid lies along the lower edge, its broadest part lying posteriorly and below the glenoid facet. The anterior margin of the lower region of the scapula is overhung by a ridge, just as in recent forms. Below this ridge, the concave surface afforded attachment for a large muscle, the scapulo-humeralis posterior.

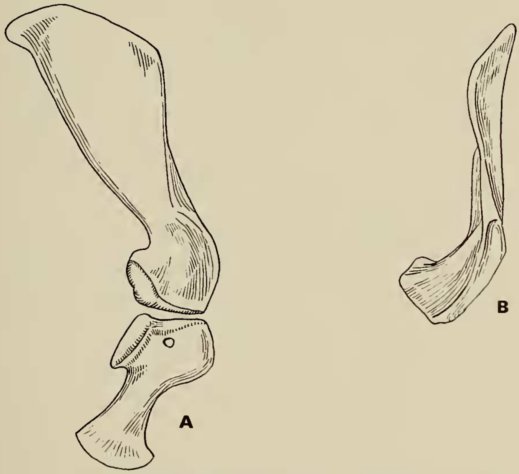

Fig. 12. *Orthosuchus stormbergi.* Pectoral girdle (natural size). A. Lateral view of right side. B. Anterior view of left scapula.

The coracoid is half as long as the scapula. Its upper region is expanded to match the lower end of the scapula, while the posterior margin is thickened to form the lower half of the glenoid. In front of this lies a prominent coracoid foramen. Distally the coracoid flares out to form a blade-like inferior end. The long axis of the coracoid, like that of the scapula, lies obliquely orientated so that in life the bone would have been directed inwards.

The sternum and interclavicle are unknown, and were presumably cartilaginous in life.

Fore-limb (Figs 13–14)

The fore-limb is completely known from the left side and, in addition, part of the lower right fore-limb is present.

In general shape the humerus is remarkably similar to that of living crocodiles. The shaft is well developed and slender. It is twisted along its length, so that with the proximal expansion lying antero-medially, the distal expansion faces antero-laterally. In living crocodiles the proximal and distal expansions lie more or less in the same plane.

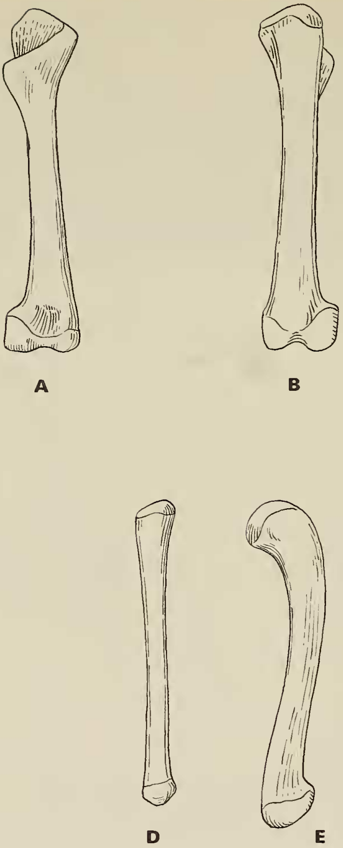

Fig. 13. *Orthosuchus stormbergi.* Fore-limb (natural size). A–C. Left humerus. A. Anterior. B. Posterior. C. Lateral views. D. Lateral view of the radius. E. Lateral view of the ulna.

In both *Orthosuchus* and in living crocodiles, the proximal expansion is of moderate size, although in recent forms it extends farther medially. The articular surface lies along the upper posterior edge and is oval in shape. The deltopectoral crest originates on the lateral edge of the proximal expansion and curves obliquely down across the anterior face of the shaft. This crest is more strongly developed in *Orthosuchus* than it is in living crocodiles, and encloses a deeper concavity on the anterior surface of the humerus. Distally the bone is thickened into two condyles. The capitellum is marginally the larger of the two, and is separated from the trochlea by a shallow groove. There is little projection of ectepicondyle or entepicondyle, and distal foramina are lacking.

The radius is a slender bone. Proximally it is thickened where it touches and partly obscures the proximal expansion of the ulna. The ulna extends beyond

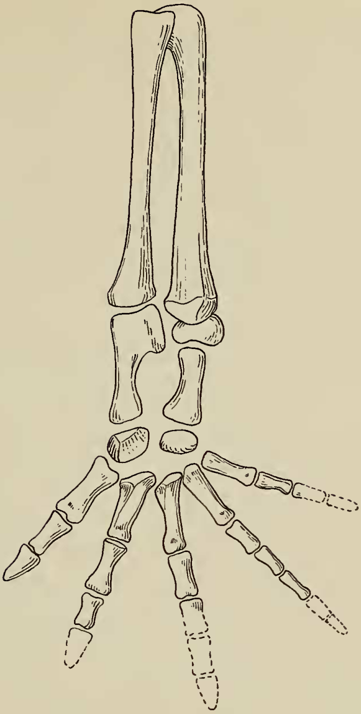

Fig. 14. *Orthosuchus stormbergi.* Lower fore-limb (natural size). Anterior view of the left radius, ulna, carpus and manus.

the limit of the radius, but it does not form an olecranon. The facet for the humerus is terminal. The articular surface of the ulna faces both forward and upward.

Distally the radius is expanded medio-laterally and forms an oval articular surface for the radiale. The ulna is also expanded distally, but in the antero-posterior direction. The ulna articulates distally with the pisiform and ulnare, and meets the radiale internally.

As in modern crocodiles, the radius is the shortest of the long bones while the ulna is the next shortest. However, the proximal part of the fore-limb is only marginally longer than the distal, the length of the radius being 88% that of the humerus. As is typical of archosaurs, the ulna is stronger than the radius and would have carried the major part of the weight borne by the fore-limb.

The carpus shows the same remarkable degree of specialization found in modern crocodiles, for the radiale and ulnare are elongated and so add an extra segment to the fore-foot. Of the two, the radiale is the longer and stouter element. Proximally the radiale is greatly enlarged to a triangular head which articulates with both radius and ulna. Consequently the weight of the body could be transmitted from both the ulna and radius through the radiale to the middle and inner digits. The pisiform is a large, flat, kidney-shaped bone which interposes posteriorly between the ulna and ulnare.

The distal row of carpals consists of two elements and these are not elongated. The larger of the two is somewhat angular and lies distal to the radiale. This presumably represents a fusion of distal one and a centrale. The second is more elliptical in shape, and is formed by fusion of distals three and four. In modern forms, generally, only one distal carpal is ossified though two other cartilaginous elements may be present.

Despite the fragile nature of the manus, five digits are known. However, only the first of these is complete, although very little is missing from the second, fourth and fifth. About half of the third digit is lacking. Clearly, the first digit is both the shortest and the stoutest, and the fifth the weakest. Further, the second and fourth digits are longer than the first, and digit three was probably the longest.

Each metacarpal is expanded proximally. The first has a shallow articular surface for the medial distal carpal, which also meets flat articular surfaces on metacarpals two and three. The proximal articular surfaces on the fourth and fifth metacarpals are in articulation with the lateral distal carpal. The metacarpals overlap one another proximally from medial to lateral sides. Each metacarpal is also expanded distally and forms a convex articular surface.

Similarly, the phalanges form articular surfaces that are concave proximally, and convex distally. The first digit bears two phalanges, the terminal phalanx being a claw. The second digit has two phalanges and the proximal part of a third. Probably this terminal phalanx is a claw, though it is impossible to be sure. Of the third digit, only the proximal phalanx and part of the next are known. The fourth and fifth digits are very weak, and because of this the number of phalanges present in each case cannot be determined with any certainty. Probably three phalanges of the fourth, and two of the fifth, are known. The phalangeal formula was probably 2, 3, 4, ?5, 3.

Pelvic girdle (Fig. 15)

The pelvis is complete, although some fragments of bone are missing. The left pubis was removed to make it possible to clean all the vertebrae. It originally occupied a position that could have been little changed from the one held in life. The right pubis is still *in situ*, but it is displaced from the pelvis. The ilium on that side is somewhat compressed dorso-ventrally.

The pelvic girdle is remarkably crocodilian in form in that the pubis is excluded from the acetabulum by the ischium. The acetabulum is large and deep, and is perforated ventrally. Dorsally a very prominent ridge, the supra-acetabular buttress, overhangs the acetabulum. In life the femur would have exerted its thrust against this.

Above the buttress, the blade of the ilium is narrow and is produced

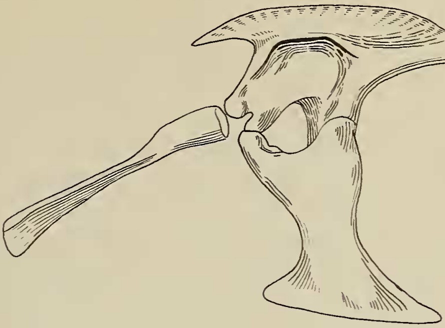

Fig. 15 *Orthosuchus Stormbergi.* Pelvic girdle (natural size). Lateral view of left side.

anteriorly to form a long, pointed process. This process is reduced in living crocodiles. Posteriorly the ilium forms a more robust post-acetabular process, much as in living crocodiles. The outer surface of the blade of the ilium, both above the supra-acetabular buttress and on the post-acetabular process, is covered by a series of fine striations. In life, the major extensor of the leg musculature, the m. ilio-tibialis and the smaller extensor, the m. ilio-fibularis, would have originated here, as would the powerful abductor, the m. ilio-femoralis.

Ventrally the ilium forms two stout processes which between them form the roof and walls of the acetabular opening. The most anterior of these bears two rounded facets, the upper of which articulates with the pubis; the lower meets the pubic process of the ischium. The posterior process bordering the acetabulum also meets the ischium.

Internally, the visible surface of the ilium is smooth, although apart from a very short median region, the whole of the internal acetabular and post-acetabular surfaces are supported by a very firm union with the two sacral ribs (Fig. 10).

The long axis of the ischium passes obliquely back in the dorso-ventral plane. The main sutural contact with the ilium is posterior, and in this region the ischium is thickened to form a broad margin to the postero-ventral edge of the acetabulum. The ischium also sends forward a narrow pubic process which curves round the ventral and ventro-lateral margin of the acetabulum. It bears a rounded surface on its leading edge for articulation with the pubis, and above this for the ilium.

Below this the ischium forms a short, narrow shaft. On both sides the ischia are fractured at this point, reflecting the distortion of the pelvis. Distally the ischium is expanded, particularly posteriorly, and its lower margin is striated. The ischia meet ventrally in the midline.

The pubis is a remarkably rod-like element, flattened on its lateral surface. It is nearly as long as the ilium and is longer than the ischium. Proximally the head is slightly expanded and bears a large articular surface for the ilium. Below this lies a smaller surface for articulation with the pubic process of the ischium. In modern crocodilians contact with the ilium has been lost and the pubis articulates only with the ischium.

Behind the articular surface there is a shallow depression laterally on the head of the pubis. This area represents the pubic rim, which is well developed in early reptiles, and is seen in forms like *Howesia.* Below this there is torsion in the pubic shaft so that proximal and distal expansions are at right angles to each other. The distal expansion is not great, though it is almost twice the size of the proximal expansion. Clearly the pubes were not fused distally to form a pubic plate, but it is probable they met distally in cartilage, as they do in modern crocodiles.

Hind-limb (Figs 16–17)

Unfortunately, both femora are broken. The break in the right femur was restored in the field, and very little of this bone can be missing. Assuming the estimated femur length to be correct, then it is still the longest of the long bones, the humerus being 79% of the length of the femur.

In form the femur is very similar to that of a modern crocodile. It has a long, curved, somewhat flattened shaft with both proximal and distal ends expanded. These expansions lie more or less obliquely to one another. There is no constriction between the head and the shaft of the femur. The head has a pronounced articular surface which is convexly rounded and oval in shape. As in living crocodiles, the articular surface is developed on the upper edge of the head, but in *Orthosuchus* it extends farther medially.

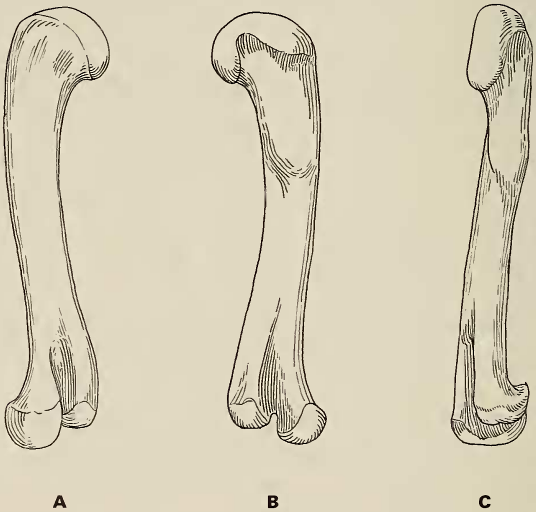

Fig. 16. *Orthosuchus stormbergi.* Reconstruction of the right femur (natural size). A. Anterior. B. Posterior. C. Medial views.

Proximally on the posterior face of the femur a shallow depression is present. This area represents the intertrochanteric fossa. Adjacent to this the lateral margin of the bone is thickened and possibly represents the remnants of the internal trochanteric crest. This area carries the insertion of the m. pubo-ischio-femoralis externus. There is no development of the greater trochanter and the ilio-femoralis musculature inserted farther down the shaft.

A thickening of bone towards the medial edge on the posterior surface of the shaft represents the fourth trochanter, to which was attached the coccygeo-femoral = caudifemoral musculature. The ratio of the distance from the proximal end of the femur to the centre of the fourth trochanter, over the distance from the distal end to the centre of the fourth trochanter in *Orthosuchus* is 0,46. In a large specimen of *Crocodylus acutus* it is 0,55, but in two small specimens of *Alligator mississippiensis* the ratio is the same as that for *Orthosuchus*. The distal condyles of the femur of *Orthosuchus* are well developed, the lateral being the larger of the two.

The left tibia and fibula are entire, and are in articulation with the tarsus and proximal pes. The proximal part of the right tibia, together with an impression of the fibula, is in articulation with the femur. The distal parts of these bones are in articulation with the astragalus and calcaneum.

The tibia is the stouter of the two bones and is particularly well developed for articulation with the femur. It is expanded posteriorly to form a large articular surface for the medial condyle of the femur, and also extends laterally to contribute to the articular surface for the lateral condyle. The fibula is modestly expanded posteriorly to complete this surface. Both articular surfaces are concave. The shaft of both the tibia and fibula is circular in cross-section in the mid-region, but lower down the inner surface becomes gently concave on the tibia and flat on the fibula.

Distally the tibia is again more developed than the fibula. Laterally the tibia is about equal in length to the fibula, but it extends farther down medially to form a large area for articulation with the astragalus. The distal articular surface of the tibia is rounded medially and has a flat, sloping lateral surface. This follows a similar contour on the upper face of the astragalus. The fibula articulates with the astragalus medially in a more or less vertical plane, and with the calcaneum ventrally where its articular surface is slightly concave.

The tibia and fibula are marginally shorter than the femur, the length of the tibia being 94% that of the femur. The fore-limb is distinctly shorter than the hind when only the long bones are considered. However when the length of the radiale is taken into account, the fore-limb is 91% the length of the hind.

The astragalus and calcaneum of *Orthosuchus* are identical in shape with these bones in living crocodiles. The astragalus is a very large element which occupies both the medial and mid-region of the tarsus. It is somewhat flattened in the mid-region, although on its medial border it is thickened and forms an oval convexity anteriorly. The calcaneum is a small, rectangular element anteriorly, but posteriorly it forms a very prominent tuber. On its posterior face

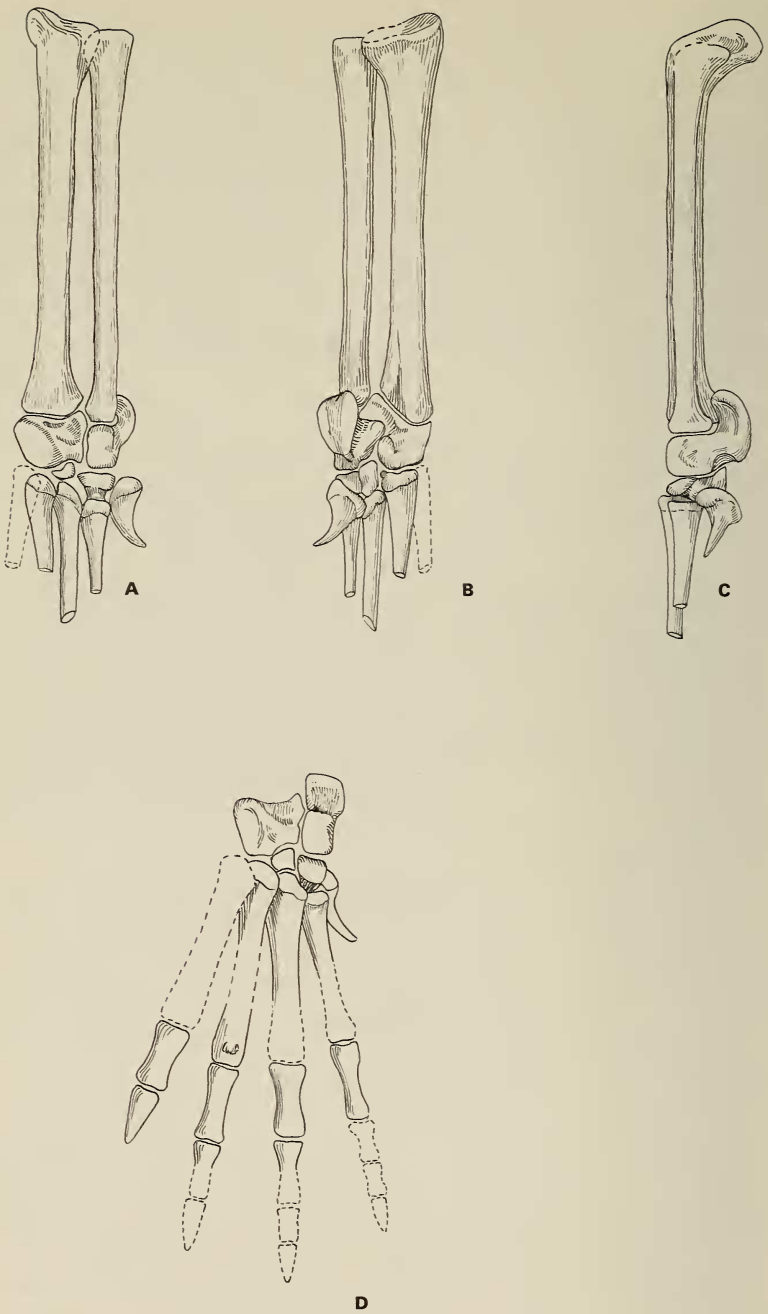

Fig. 17. *Orthosuchus stormbergi.* Lower hind-limb (natural size). A–C. Left tibia and fibula, tarsus and metatarsus, as preserved. A. Anterior. B. Posterior. C. Lateral views. D. Reconstruction of left tarsus and pes.

the tuber is grooved vertically for the passage of the gastrocnemius tendons. The calcaneum also extends obliquely up over the posterior surface of the astragalus.

The astragalus articulates on its upper surface both with the expanded distal end of the tibia and with the medial surface of the fibula, the major articulation here being between the astragalus and tibia. The astragalus also articulates with the calcaneum. Superficially this articulation would seem to be identical with that found in modern crocodiles and probably, as in these forms, a small ball and socket articulation exists between these two bones. Movement between them is therefore in the vertical plane and the joint is a crurotarsal one, with the astragalus functioning with the crus, and the calcaneum with the pes. In contrast to the articulation between tibia and astragalus, that between the fibula and calcaneum is a freely movable one.

The astragalus articulates distally with the innermost of two distal tarsals and metatarsal two. It clearly also met metatarsal one, though this is known only from an impression. The calcaneum articulates distally with the lateral distal tarsal. The tarsalia of *Orthosuchus* occupy the same position in the tarsus as is found in living crocodiles.

The medial tarsal is the smaller of the two, and meets metatarsals two and three distally. Presumably it represents tarsal three. The larger lateral tarsal extends posteriorly and is probably tarsal four. Posteriorly it meets metatarsal five, anteriorly it meets metatarsal four and just touches metatarsal three.

The metatarsals overlap one another proximally from medial to lateral surfaces. The third seems to be the stoutest. The fifth is reduced to a hook-like element which quite clearly lacks phalanges and is held behind the third and fourth metatarsals. All the elongate metatarsals are incomplete, although the distal end of one was found in association with a few phalanges of the left pes overlying the mid-dorsal ribs. This is most likely part of metatarsal two, and the digits are preserved in inverted sequence in relation to their metatarsals. The distal end of the metatarsal is grooved on its dorsal surface near to the articular region. Of this second digit, one phalanx and part of a second are known. A phalanx and claw of digit one is present, although metatarsal one is known only from an impression. One phalanx from each of digits three and four are known. The proximal articular surface of each of these is concave, and its distal end rounded.

BODY ARMOUR (Fig. 18)

Dorsally the body is covered by a double row of large rectangular scutes. Neither ventral nor lateral scutes are present, nor is there any evidence which suggests that the body was protected ventrally in this way. Virtually nothing remains of the scutes of the caudal region.

The number of scute pairs corresponds to the number of vertebrae present. In addition, a very small scute is present at the extreme anterior end of the trunk, and this could correspond to the pro-atlas. The scutes increase in length,

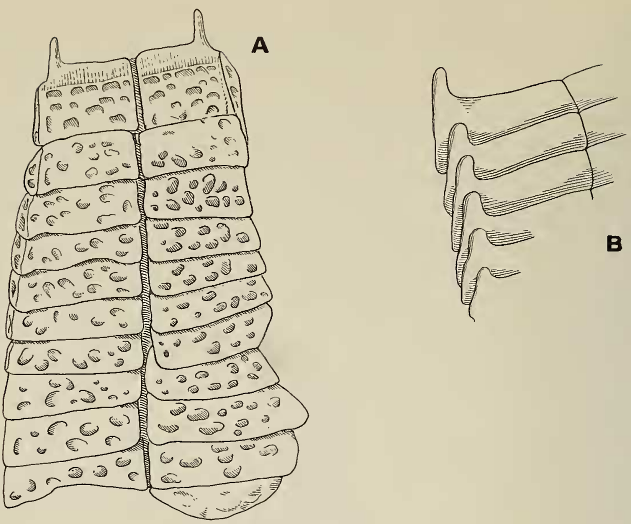

Fig. 18. *Orthosuchus stormbergi.* Dorsal scutes (natural size). A. Dorsal view of anterior scutes, the most anterior pair are figured entire. B. Ventral view of cervical scutes.

passing back along the length of the body in an identical manner to that which occurs in the vertebrae. Hence, the scutes are shortest antero-posteriorly in the cervical, and longest in the sacral region. A broadening of the scutes also occurs back to the anterior dorsal series. Behind this they decrease in width. In the sacral region their exposed dorsal surfaces are rectangular in shape.

The posterior edge of each scute overlies and conceals the anterior edge of the following scute. Approximately one-third of the length of each scute is concealed in this way. Where this border is visible it is seen to be smooth, while the exposed surface of each scute is sculptured by a system of deep pits which form a pattern similar to that on the skull. The extreme outer edge of each scute bends sharply down to form a narrow lateral part. In this way, a sharp ridge borders the lateral margin of each scute dorsally. In the cervical and dorsal regions the outer anterior edge of each scute extends forwards as a blunt, peg-like process which lies below the preceding scute.

MYOLOGY OF *ORTHOSUCHUS*

Although the restoration of musculature in an extinct reptile must always involve an element of uncertainty, it seems likely that in *Orthosuchus* the muscle arrangement could not have been very different from that found in living crocodiles. The nomenclature used throughout follows that of Romer (1956), and where this differs from that used by other workers in this field, their nomenclature has been cited in parentheses.

Table 2

Measurements of the skull and postcranium in mm

	K4639	K409
Length of skull, front of snout to parietal/supraoccipital suture	54,0	90,0
Preorbital length, front of snout to anterior margin of orbit	25,0	46,0
Maximum breadth of skull across external borders of quadratojugals	38,0	70,7
Breadth of cranial table at mid-level of superior temporal fenestrae	33,0	55,0
Breadth of intertemporal region at mid-level of superior temporal fenestrae between their inner borders	6,0	6,0
Breadth of interorbital region at mid-level between inner borders of orbits	11,0	16,0
Breadth of posterior region of the snout immediately anterior to orbits	*ca* 4,5	26,0
Breadth of anterior region of snout across premaxillae	10,0	17,4
Maximum length of superior temporal fenestra	10,0	19,0
Maximum length of inferior temporal fenestra	—	21,0
Maximum height of inferior temporal fenestra	—	12,0
Maximum length of orbit	13,0	17,0
Maximum length of antorbital fenestra	—	13,0
Distance between tip of snout and anterior border of choana	—	21,6
Length of lower jaw	—	*ca* 110,0
Length of mandibular symphysis	—	9,0
Length of external mandibular fenestra	—	34,0
Maximum height of scapula	—	46,0
Maximum height of coracoid	—	23,0
Maximum length, antero-posteriorly, of superior scapula	—	*ca* 22,0
Maximum length, antero-posteriorly, of inferior coracoid blade	—	11,2
Length of humerus	—	45,0
Length of radius	—	39,5
Length of ulna	—	43,1
Length of radiale	—	16,3
Length of ulnare	—	10,0
Length of metacarpal 1	—	9,0
Length of metacarpal 2	—	9,8
Length of metacarpal 3	—	10,5
Length of metacarpal 4	—	9,0
Length of metacarpal 5	—	7,3
Length of digit 1	—	20,5
Maximum length of iliac blade	—	36,8
Height of ilium above acetabular fenestra	—	12,5
Maximum height of acetabulum	—	15,3
Length of pubis	—	33,5
Breadth of distal pubis	—	9,0
Height of ischium	—	22,0
Length of ventral ischial margin	—	24,0
Length of femur	—	*ca* 57,0
Distance between proximal femur and centre of fourth trochanter	—	18,0
Length of tibia	—	53,5
Length of fibula	—	51,0
Length of metatarsal 5	—	9,5

MUSCULATURE OF THE HEAD (Fig. 19)

A general account of the facial musculature of crocodilians given by Von Wettstein (1937) was found helpful in this analysis. In addition, Anderson (1936) based the reconstruction of the jaw musculature of the phytosaur *Machaeroprosopus* on that of modern reptiles, particularly *Alligator* and

Spenodon. Colbert (1946) also applied the myology of the head of living crocodiles to that of the crocodilian *Sebecus.*

It is generally agreed that in Crocodilia the m. adductor mandibulae separates into the external, posterior and internal portions as tabulated below, though Edgeworth (1935) failed to identify a posterior (= medial of Edgeworth) portion.

Jaw muscles of the Crocodilia based on the nomenclature of Lakjer (1926) *and Anderson* (1936)

Innervated by the trigeminal	
	superficialis
Adductor mandibulae externus	medialis
	profundus
Adductor mandibulae posterior	
	pseudotemporalis
	pterygoideus dorsalis = pterygoideus D of Lakjer
Adductor mandibulae internus	
	pterygoideus ventralis
	intramandibularis
Innervated by the facial	
Depressor mandibulae	

The m. adductor mandibulae externus was probably divisible into three muscle sheets in *Orthosuchus* as in living crocodiles. In modern genera the m. mandibulae externus superficialis arises along the outer edge of the quadrate between the jaw articulation and the postorbital, and inserts on the dorsal surface of the surangular. There is no reason to suppose that this muscle had a different arrangement in *Orthosuchus.* However, this muscle presumably inserted mainly on the horizontal flange of the surangular of *Orthosuchus.* It is also likely that the m. adductor mandibulae externus medialis occupied a similar position in *Orthosuchus* to that seen in *Alligator.* It probably arose partly from the ventral surface of the postorbital and partly from the pterygoid face of the quadrate deep to the superficial sheet of the m. adductor mandibulae externus. The m. adductor mandibulae externus medialis would also have inserted on the dorsal surface of the surangular underneath the superficial sheet.

Deeper again and running below the m. adductor mandibulae externus medialis lies the m. adductor mandibulae externus profundus. This is the only muscle to penetrate the superior temporal fenestra. Without doubt the major origin of this muscle in *Orthosuchus*, as in *Alligator*, must have been from the parietal, squamosal and quadrate within the superior temporal fossa, though other slips may have attached more ventrally to the quadrate and postorbital. Similarly the major insertion of this muscle in *Orthosuchus* must have been into the membrane lying over the adductor fossa.

In *Orthosuchus* both the temporal fenestrae and the adductor fossa are very large relative to the length of the skull. Indeed they are larger in *Orthosuchus* than they are in all the living crocodiles, including *Gavialis*. The large floored area of the superior temporal fossa indicates that the m. adductor mandibulae externus profundus had a much larger insertion area in *Orthosuchus* than it has in living crocodiles. Further the large size of the inferior temporal fenestra and adductor fossa suggest that this muscle required a larger area in which to bulge. It therefore seems probable that the m. adductor mandibulae externus profundus was larger and more powerfully developed in *Orthosuchus* than it is in living forms.

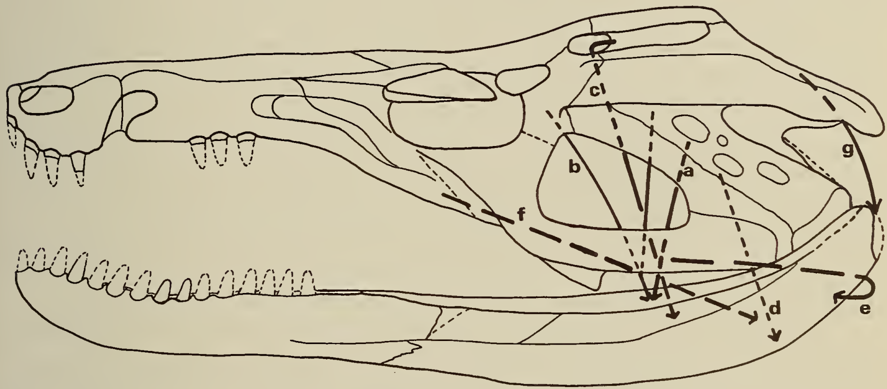

Fig. 19. *Orthosuchus stormbergi*. Diagrammatic reconstruction of the inferred general location of the jaw muscles.

Abbreviations: a: m. adductor mandibulae externus superficialis; b: m. adductor mandibulae externus medialis; c: m. adductor mandibulae externus profundus; d: m. adductor mandibulae posterior; e: m. pterygoideus ventralis; f: m. pterygoideus dorsalis; g: m. depressor mandibulae.

The second part of the adductor, the m. adductor mandibulae posterior, no doubt also occupied a similar position in *Orthosuchus* to that seen in living crocodiles. It must have been a short, stout muscle which attached to the pterygoid face of the quadrate, and then ran slightly obliquely down to the lower jaw. In living crocodiles this muscle inserts on the lower surface of the angular along the posterior part of the external mandibular fenestra, and on the inner wall of the angular medial to this fenestra. Since the angular does not extend medially in *Orthosuchus* as it does in living genera, it seems likely that this muscle inserted in part on the prearticular.

In *Alligator* the m. adductor mandibulae posterior is divided at its insertion by the m. pseudotemporalis. Probably a similar arrangement existed in *Orthosuchus*. This muscle would have originated on the postorbital.

The second part of the m. adductor mandibulae internus, the m. pterygoideus, is extremely large in living crocodiles. There can be little doubt that in

Orthosuchus it arose mainly from the posterior edge of the pterygoid flange. It probably also attached to the ectopterygoid, and to the basisphenoid and adjacent medial portion of the pterygoid, as it does in living crocodiles.

In eusuchians a ventral slip of the m. pterygoideus wraps round the lower jaw and inserts on the retroarticular process, below and behind the glenoid. Since this process is absent in *Orthosuchus* a comparable muscle must have had a more anterior insertion principally in front of the glenoid. The ventro-lateral surface of the posterior region of the angular of *Orthosuchus* indicates an area of muscle attachment in life. This is suggested as the insertion area of the m. pterygoideus ventralis. In this position the muscle would have acted more or less at right angles to the lower jaw when this was widely open, and would have been efficient in closing the jaws. The migration of the m. pterygoideus ventralis on to the retroarticular process in later crocodiles has reduced its efficiency in closing the jaw. However, as Ewer (1965) has pointed out, a muscle in this position stabilizes the articulation.

In living crocodiles it is the powerfully developed anterior extension of the pterygoideus, the m. pterygoideus dorsalis (= the pterygoideus D of Lakjer), that serves to close the lower jaw. This muscle originates along the length of the inner surface of the snout. Anteriorly it extends well in front of the orbit, and attaches to the dorsal surface of the maxilla, palatine and pterygoid. It inserts on the medial surface of the angular, below and in front of the glenoid.

In view of the large pterygoid flange present in *Orthosuchus* it is probable that some development of the m. pterygoideus dorsalis had occurred. However it could not have been as extensive in *Orthosuchus* as it is in eusuchians. Probably it originated from the dorsal surfaces of both the pterygoid and palatine, but it could not have extended any farther forward than the anterior margin of the orbit in view of the limited development of the bony secondary palate. Posteriorly it probably attached to the membrane over the very large adductor fossa, and may have inserted on the prearticular.

The evidence suggests that the m. pterygoideus ventralis and the m. pterygoideus dorsalis were not as well developed in *Orthosuchus* as they are in living crocodiles. Nevertheless this muscle must have been considerable, as shown by the large size of the pterygoid flange. Further, the positioning of this muscle suggests that it was fully effective in closing the jaws. On the other hand, the large size of the superior temporal fenestra clearly indicates that the m. adductor mandibulae externus profundus was also extensive, as it is in *Gavialis*, so increasing the efficiency of snapping shut the jaws.

Dollo (1884) related the development of this musculature to the size of the antorbital fenestra. He concluded that where the m. adductor mandibulae externus was more important than the m. pterygoideus dorsalis, the antorbital fenestra was reduced. Conversely this fenestra was enlarged where the m. pterygoideus dorsalis was well developed. Gregory & Adams (1915) and later workers supported this idea. Walker (1961) expressed the opinion that in *Ornithosuchus* the m. pterygoideus dorsalis originated in large part from a membrane stretched across the depressed area on the snout surrounding the antorbital fenestra, and probably also from the depressed area itself.

Certainly the small size of the antorbital fenestra may be correlated to the greater importance of the m. adductor mandibulae externus profundus in *Orthosuchus*. On the other hand, Ewer (1965) has pointed out that in all later crocodiles it is the m. pterygoideus dorsalis that is the more extensive of the two muscles, yet the antorbital fenestra has been lost. This would not have occurred had the fenestra been the main area of origin of the muscle. There seems little doubt that in *Orthosuchus* the antorbital fenestra was unrelated to the jaw musculature. It probably housed a gland in life.

According to Lakjer (1926) and Anderson (1936), the m. intramandibularis is differentiated from the m. adductor mandibulae in living crocodiles. This muscle arises from the membrane lying over the adductor fossa, and then passes over the coronoid through the Meckelian fossa and along the primordial canal to insert on Meckel's cartilage. In Anderson's view, since the m. adductor mandibulae externus profundus and the m. pterygoideus dorsalis have slips which attach to the m. intramandibularis, the anterior insertion of this muscle increases the efficiency of the other muscles. It is possible that a similar muscle was present in *Orthosuchus*, although presumably it passed over the prearticular before entering the jaw.

In view of the insignificant development of the retroarticular process in *Orthosuchus*, it seems probable that the m. depressor mandibulae was not strongly developed. No doubt it had a similar arrangement to that seen in living crocodiles, and arose on the occipital surface of the parietal, squamosal and exoccipital, and inserted on the posterior margin of the articular. In living crocodiles where the retroarticular process is prominent, the m. depressor mandibulae is correspondingly strongly developed. Adams (1919) suggests that since crocodiles generally lie with their heads on the ground, this muscle serves to lift the cranium rather than lower the bottom jaw. It may be that this muscle was less well developed in *Orthosuchus*, and that the skull did not reach the massive size attained by many of the living species.

MUSCULATURE OF THE SHOULDER AND FORE-LIMB (Figs 20–21)

Fürbringer (1876, 1900) described in detail the musculature of the shoulder and upper arm of various reptiles, and this work was followed by Von Wettstein (1937) in his account of the Crocodilia. Gregory & Camp (1918) also reviewed the identification of the shoulder muscles. This account follows the terms used by these workers.

Axial muscles associated with the pectoral girdle

The pectoral girdle of *Orthosuchus* differs from that of living crocodiles in that while the scapula is long, relative to the size of the humerus, the coracoid is shorter. Presumably, therefore, attachment areas of certain muscles would have differed from those occurring in living crocodiles. On the other hand a clavicle is lacking in *Orthosuchus*, as it is in living crocodiles, and it seems likely that specializations in the axial musculature which are associated with this bone's absence in modern genera had already taken place in *Orthosuchus*.

In *Orthosuchus* the m. capito-dorso-clavicularis (= trapezius of Fürbringer) probably arose from the parietal and squamosal, and merged posteriorly into the m. latissimus dorsi, as it does in recent crocodiles. The m. sterno-mastoideus consists of two parts in crocodiles. The muscle arises on the skull, but is divided by the atlantal rib before it inserts on the sternum. Presumably this muscle was similarly modified in *Orthosuchus*, since a well-developed atlantal rib is present.

Although it is not found in other living reptiles, the m. rhomboideus is developed in the Crocodilia. It arises from the fascia above the eighth and ninth cranial nerves, and inserts on the anterior two-thirds of the dorsal inner surface of the supra-scapula. Since this muscle is also well developed in birds, it seems probable that it was present in ancestral archosaurs. In *Orthosuchus* the large size of the scapula suggests that the rhomboideus muscle may have inserted principally on this element rather than on the supra-scapula. Similarly, it seems probable that the deeper m. levator scapulae superficialis inserted on the upper anterior external margin of the scapula in *Orthosuchus*. The surface of this margin shows fine striations which possibly indicate muscle attachment areas. The muscle presumably took origin on the cervical vertebrae.

In living crocodiles the m. serratus superficialis arises on the last cervical and first three dorsal ribs, behind the pectoral girdle and below the m. latissimus dorsi. There is fundamentally no difference between these ribs in *Orthosuchus* and those of living crocodiles. However, whereas in living species the 'uncinate' processes are normally cartilaginous, in *Orthosuchus* they are fully ossified. This muscle most likely inserted on the posterior margin of the scapula. Similarly, the deep-lying m. serratus profundus presumably arose from the transverse process of the cervical vertebrae, and inserted on the inner and upper surface of the scapula. The m. omohyoid must also have inserted on to this surface of the scapula.

Dorsal muscles of the fore-limb

The m. latissimus dorsi is weakly developed in modern crocodiles and shows some differentiation into two parts. In *Orthosuchus* it would have taken origin from the external surfaces of the dorsal ribs and inserted on the head of the humerus near its posterior margin. Almost certainly the m. subcoraco-scapularis (= subscapularis) inserted near to this muscle, and arose from the rear edge of the scapula. Similarly, it is likely that the m. teres major was present in *Orthosuchus*. According to Fürbringer, although this muscle is absent in *Sphenodon*, and occurs in only a few lacertilians (Agamidae), it is developed in living crocodilians. In *Orthosuchus* the upper, backwardly projecting margin of the scapula probably acted as the area of attachment for this muscle, which extended beneath the m. latissimus dorsi to insert on the lateral surface of the humerus.

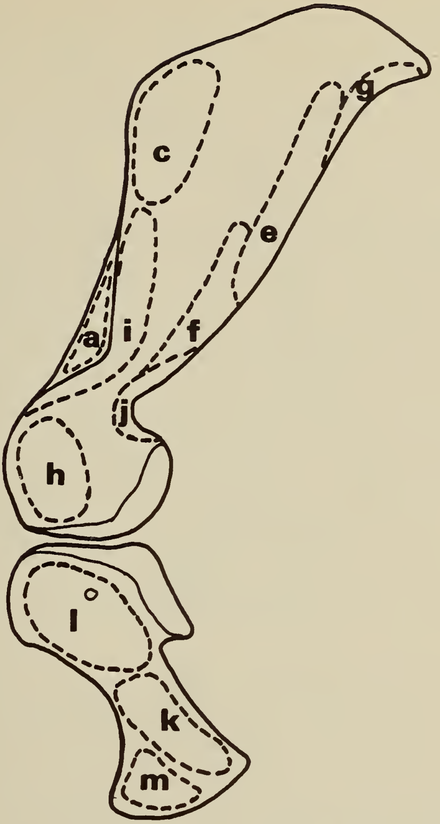

Fig. 20. *Orthosuchus stormbergi.* Lateral surface of the pectoral girdle showing inferred general areas of muscle attachments.

Abbreviations: a: m. trapezius; b: m. rhomboideus; c: m. levator scapulae superficialis; d: m. latissimus dorsi; e: m. serratus superficialis; f: m. subscapularis; g: m. teres major; h: m. scapulo-humeralis posterior; i: m. dorsalis scapulae and m. deltoides clavicularis; j: m. triceps; k: m. coracobrachialis brevis; l: m. supracoracoideus; m: m. biceps brachii.

In living crocodiles the m. scapulo-humeralis anterior is lacking, though the posterior division is well developed. A similar arrangement almost certainly existed in *Orthosuchus*, since there is a well-marked depression ventrally on the external surface of the scapula, near to its anterior border. A similar area on the scapula of living crocodiles marks the origin of this muscle. The m. scapulo-humeralis posterior (= scapulo-humeralis profundus of Fürbringer) would have inserted on the lateral surface of the humerus. In *Orthosuchus* this area of the humerus is marked by fine striations.

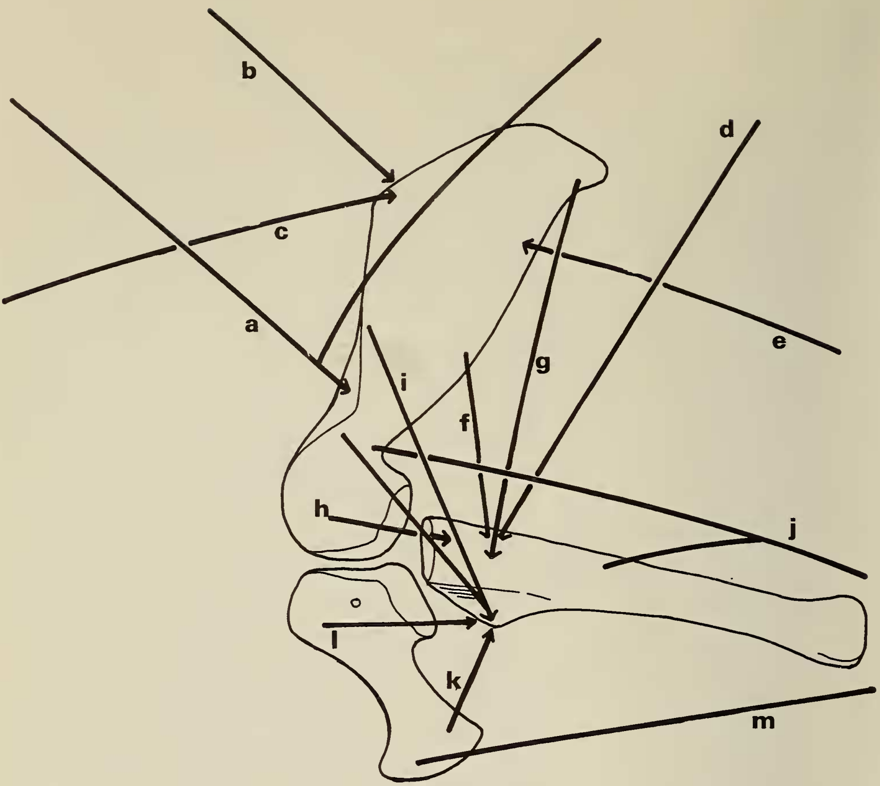

Fig. 21. *Orthosuchus stormbergi.* Diagrammatic reconstruction of the inferred main lines of action of the muscles of the fore-limb. Abbreviations as in Figure 20.

The deltoid muscle in reptiles is typically a broad but thin sheet which arises in two parts: one, the m. dorsalis scapulae (= deltoides scapularis superior of Fürbringer), arises from the upper part of the scapula, and the second, the m. deltoides clavicularis (= cleido-humeralis), from the clavicle and interclavicle. Since the clavicle has been lost in crocodiles, the m. deltoides clavicularis has shifted its origin to the scapula. A similar arrangement must have existed in *Orthosuchus*, and both parts of the deltoid would have inserted on the outer surface of the deltopectoral crest. Fine striations indicate this area as one of muscle attachment in life.

Despite the absence of an olecranon process in living crocodilians, the major dorsal muscle of the arm, the m. triceps, still forms a massive muscle body. In view of this, and since the proximal end of the ulna is expanded in crocodilian fashion, there is no reason to suppose that the m. triceps was not well developed in *Orthosuchus*. It is also likely that the areas of attachment of this muscle on to the pectoral girdle and humerus were fragmented into five centres of origin, as they are in living crocodiles. In these forms the muscle consists of two layers, the deeper of which arises from the upper, posterior and medial surfaces of the humerus, and the outer having its origins on the pectoral girdle. In *Orthosuchus* the scapula is grooved above the glenoid facet, and very probably this area denotes in part the origin of the m. triceps. The insertion of this muscle must have been by a common tendon on to the head of the ulna.

Ventral muscles of the fore-limb

The m. pectoralis in *Orthosuchus* no doubt formed a well-developed superficial muscle layer, originating on the interclavicle and ribs and inserting on the apex of the deltopectoral crest.

In living crocodiles the longus division of the m. coracobrachialis is absent and a similar arrangement was probably present in *Orthosuchus*, since distally the humerus resembles that of extant forms. Probably the m. coracobrachialis brevis would have arisen on the postero-ventral margin of the coracoid. However, this area of attachment must have been relatively smaller than that found in living crocodiles, since distally the coracoid is neither as elongate nor as expanded in *Orthosuchus* as it is in the eusuchians. This muscle would have inserted in the concavity antero-medial to the deltopectoral crest, as it does in living species. Again, its area of insertion must have been more limited in *Orthosuchus* than in modern crocodiles, judging by the more robust nature of the deltopectoral crest.

According to Von Wettstein, the m. supracoracoideus in living crocodiles has partially shifted its origin on to the inner face of the coracoid and lower edge of the scapula because of the considerable development of the m. coracobrachialis. It is possible that in *Orthosuchus*, where the m. coracobrachialis was more feebly developed, the area of origin of the m. supracoracoideus was confined to an area above that of the m. coracobrachialis. The m. supracoracoideus would then have inserted on the deltopectoral crest lateral to the point of attachment for the m. pectoralis.

The outer surface of the coracoid of *Orthosuchus* must also have given origin to the m. biceps brachii, which would have inserted on to the proximal part of the radius and ulna. The m. brachialis inferior was probably well developed, and in life would have attached to the anterior margin of the humerus, and inserted on the proximal end of the ulna.

Muscles of the lower arm

The following account is based on the work of Von Wettstein, who followed Ribbing (1907), and of Haines (1939), who made a comparative study of the extensor muscles of the forearm.

In view of the marked similarity between the lower arm elements of *Orthosuchus* and that of living crocodiles, there seems every reason to suppose that the musculature of this region in *Orthosuchus* would have resembled that of eusuchians. In this group in general there is a reduction in the lower arm and hand musculature.

Typically, the long extensors of the forearm attach to the ectepicondyle of the humerus. This projection is only slightly more developed in *Orthosuchus* than it is in living crocodiles, where it is minimal. Very likely, therefore, the m. extensor digitorum communis (= humerodorsalis of Haines) was as reduced in *Orthosuchus* as it is in modern forms. In living crocodiles this muscle no longer inserts on to all the digits, but chiefly on to metacarpal two, with extensions to four and the radiale.

There can be little doubt that in *Orthosuchus* the m. supinator (= extensor antibrachii radialis of Ribbing) also arose from the ectepicondyle in two parts, as in both living crocodiles and lizards, with the m. extensores carpi radiales attaching to the radius. Similarly, the m. anconeus (= extensor antibrachii ulnaris of Ribbing) was probably well developed and also took origin on the ectepicondyle. On the other hand, the m. extensor carpi ulnaris may well have been somewhat limited in extent. In living crocodiles this muscle is confined to the ulna, and does not extend to the pisiform.

The m. abductor pollicis longus (= abductor digiti 1 of Ribbing = supinator manus of Haines) was no doubt extensively developed in *Orthosuchus*. It probably originated on the radius as well as on the ulna, and inserted on to the radiale as it does in living crocodiles. The m. extensores digitorum breves would have extended on to the digits. In Haines's view these specializations in musculature are associated with a great mobility of the wrist joint and the use of the elongated carpus as an extra limb segment.

Typically, the flexor muscles of the lower arm are more powerful than the extensors, since the main propulsive effort is a backward push of the distal part of the limb. The long flexors arise from the entepicondyle of the humerus which, although of limited development in crocodiles, is a little more pronounced and rugose in *Orthosuchus* than it is in later forms.

In living crocodiles, the m. flexor digitorum profundus (= flexor accessorius of Ribbing) is well developed, while the m. flexor palmaris superficialis (= flexor primordialis communis of Ribbing) is less extensive. This latter muscle is united with the m. flexores breves superficiales. Possibly a similar arrangement existed in *Orthosuchus*. Certainly in life this medial muscle mass would have inserted on a palmar aponeurosis and effected flexion of the toes.

In living genera the m. pronator teres (= flexor antibrachii radialis of Ribbing) is joined together with the m. supinator, but neither the m. flexor carpi radialis nor the m. epitrochleoanconeus (= antibrachii ulnaris of Ribbing) is present. Whether or not reduction of musculature had proceeded this far in *Orthosuchus* is difficult to determine. These muscles are present in lizards and *Sphenodon*, but in these forms the entepicondylar process is well developed. On balance, it seems likely that in *Orthosuchus* these muscles were at best only feebly developed.

Deep in the forearm, the m. pronator profundus, connecting radius and ulna, probably had a similar arrangement to that seen in living crocodiles, passing between the m. flexor digitorum profundus and the m. pronator teres.

As in recent genera, the m. abductor digiti V was most likely well developed, taking origin on the palmar aponeurosis and inserting on the metacarpals and phalanges of the fifth digit.

MUSCULATURE OF THE PELVIS AND HIND-LIMB (Figs 22–24)

The probable arrangement of the muscles of the pelvis and upper leg of *Orthosuchus* is based on that found in *Alligator* (Romer 1923).

Axial muscles associated with the pelvis

The dorsal axial muscles in *Orthosuchus* would have run antero-posteriorly above the lumbar and caudal transverse processes and attached to the dorsal surfaces of the sacral vertebrae and internal surfaces of the ilium.

Similarly, the ventral axial musculature must have consisted of a series of muscle sheets covering the flanks of the body. In *Alligator* the three lateral members of this series all take origin from the lumbo-dorsal fascia. This fascia arises from the surface of the dorsal musculature and from the tips of the transverse processes of the lumbar vertebrae, and attaches posteriorly to the anterior edge of the blade of the ilium. In *Orthosuchus* this area of the ilium is extended forward to form a prominent anterior process, and may have provided a stronger base of attachment for the fascia.

Presumably these lateral muscles, the m. obliquus abdominis externus, the m. obliquus abdominis internus and the m. transversus abdominis, had a similar arrangement in *Orthosuchus*. The m. obliquus abdominis externus inserts on the anterior margin of the acetabulum, the last abdominal rib and on an aponeurosis over the main part of the m. rectus abdominis. The m. obliquus abdominis internus inserts on the posterior ribs and gastralia, and the m. transversus abdominis inserts on the m. rectus abdominis. The m. rectus abdominis no doubt ran posteriorly in the ventral midline to attach principally to the gastralia and abdominal ribs, though a part of it may have inserted on the posterior edge of the pubis and on the m. ilio-ischio-caudalis, as it does in *Alligator*.

In *Orthosuchus* the posterior process of the iliac blade extends well back. Similarly, the postero-ventral edge of the ischium is produced far posteriorly. This indicates increased attachment areas for the m. ilio-ischio-caudalis. In life this muscle would have occupied the ventral half of the tail on either side between the transverse processes and the midline ventrally. It is, therefore, fairly certain that the tail was a highly muscular organ.

Troxell (1925) has pointed out that the decrease in size of the vertebrae in both directions from the pelvis in living crocodilians is of advantage to the animal in swimming, where the tail is the propelling organ. A similar change in size of the vertebrae occurs in *Orthosuchus*. Presumably the tail could act as a propulsive organ in swimming, and no doubt also assisted in movement over land. However, the nature of the articular surfaces of the centra indicates that the degree of angular movement between successive vertebrae could not have been as great as that in living crocodiles, where the vertebrae are procoelous.

Dorsal muscles of the hind-limb

Above the acetabulum, and along the upper part of the posterior process, the ilium bears a number of distinct striae which suggest an area of muscle attachment. The most dorsal of these would probably have been the m. ilio-tibialis. This constitutes one part of the major dorsal muscle of the thigh, the m. quadriceps femoris. In *Alligator*, the m. ilio-tibialis has three distinct heads, but it is impossible to determine whether a similar arrangement existed in *Orthosuchus*, or whether its origin was still undivided.

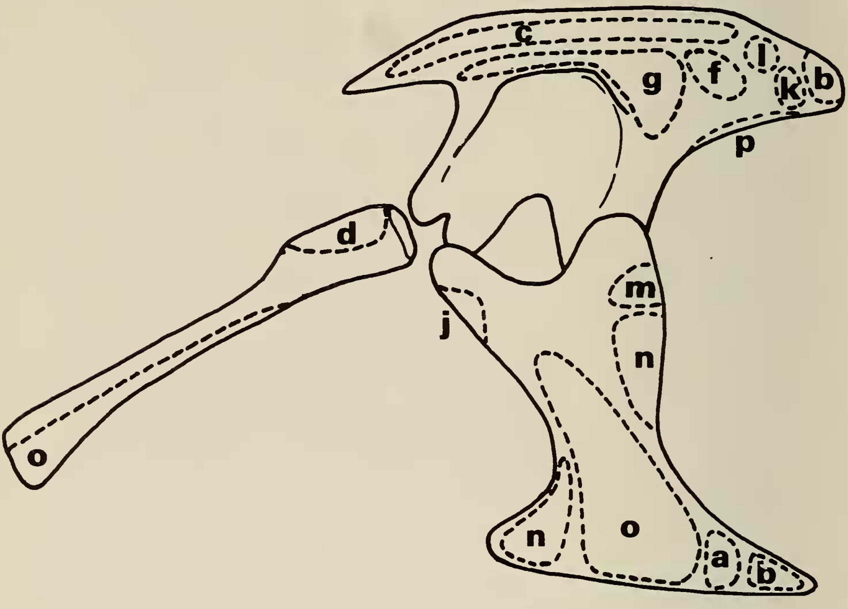

Fig. 22. *Orthosuchus stormbergi.* Lateral surface of the pelvic girdle showing inferred general areas of muscle attachments.

Abbreviations: a: m. rectus abdominis; b. m. ilio-ischio-caudalis; c: m. ilio-tibialis; d: m. ambiens; e: m. femoro-tibialis; f: m. ilio-fibularis; g: m. ilio-femoralis; h: m. ischio-trochantericus; i: m. pubo-ischio-femoralis-internus; j: m. pubo-ischio-tibialis; k: m. flexor, tibialis internus parts 1 and 2; l: m. flexor tibialis externus; m: m. flexor tibialis internus part 3; n: m. adductor femoris; o: m. pubo-ischio-femoralis externus; p: m. caudi-femoralis (= coccygeo-femoralis brevis); q: m. caudi-femoralis (= coccygeo-femoralis longus).

The m. ambiens in *Alligator* has two areas of origin. The smaller part arises on the proximal medial surface of the pubis, but the major origin is on the junction of the external surface of the pubis and the cartilage which lies in front of the acetabulum. The upper edge of the proximal end of the pubis of *Orthosuchus* is marked by a shallow depression. Very probably this denotes the area of origin of the major part of the m. ambiens. Since the proximal end of the pubis lies in a more dorsal position, the m. ambiens must have had a higher area of origin in *Orthosuchus* than it does in living crocodilians. In *Alligator* both elements of the m. ambiens unite with the m. ilio-tibialis. In addition, the larger element forms a tendon which passes through the extensor tendon of the m. ilio-tibialis across the knee to the lateral surface of the leg, where it joins the external head of the m. gastrocnemius. A similar tendon had probably been developed in *Orthosuchus*.

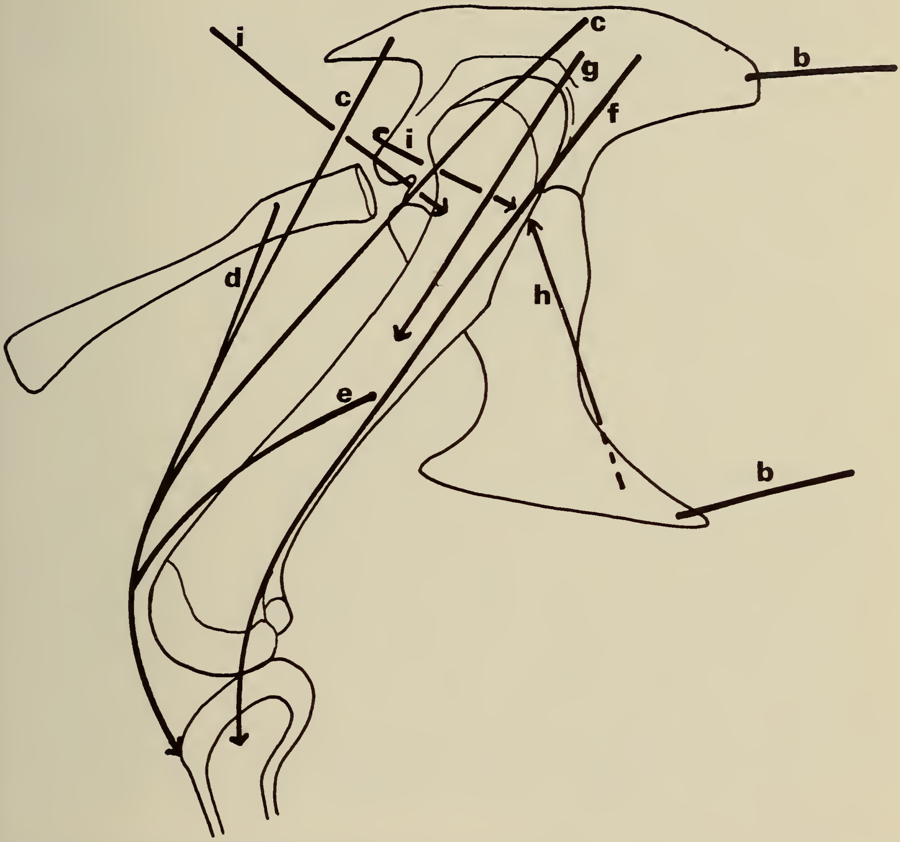

Fig. 23. *Orthosuchus stormbergi*. Diagrammatic reconstruction of the inferred main lines of action of the dorsal muscles of the thigh. Abbreviations as in Figure 22.

The anterior (= dorsal of Romer) and medial (= anterior of Romer) surfaces of the greater part of the shaft of the femur no doubt provided an attachment area for the origin of the m. femoro-tibialis, the third component of the m. quadriceps femoris. In *Alligator* this muscle has a second, more lateral (= posterior of Romer) origin, but it is impossible to determine whether this was also the case in *Orthosuchus*. Its insertion would have been on to the weakly developed cnemial crest of the tibia. Nevertheless it seems that in *Orthosuchus*, as in living crocodiles, the m. quadriceps femoris was a powerful extensor of the thigh. Presumably the m. ilio-fibularis, a smaller extensor, ran parallel to it from just below the m. ilio-tibialis, and inserted into the head of the fibula. It may also have connected to the external head of the m. gastrocnemius as it does in *Alligator*.

The blade of the ilium above the acetabulum is deeper in *Orthosuchus* than it is in *Alligator*. This expansion no doubt reflects an increased area of origin for the m. ilio-femoralis, which arises below the m. ilio-tibialis. In life this muscle would have inserted on the lateral border of the femur for the greater part of the length of the shaft, and would have been a very powerful abductor.

In *Alligator* a small muscle, the m. ischio-trochantericus, runs from the posterior part of the inner surface of the ischium and inserts at the outer anterior edge of the femur, near to its head. There is no reason to suppose that a similar muscle did not exist in *Orthosuchus*.

The m. pubo-ischio-femoralis internus primitively originates on the medial surface of the pubis. However, Romer (1923) has shown that in *Alligator* this muscle is present in two parts and has more dorsal origins. The similarity of the pelvis in *Orthosuchus* suggests that this change had already occurred. One part of the muscle probably originated from the ventral surfaces of the posterior dorsal vertebrae, and possibly also attached to the inner surface of the anterior process of the blade of the ilium. This muscle would have inserted on the anterior surface of the proximal part of the femur. The evidence of strong muscle attachment in this area is shown by fine striations marking the bone at this point. The second part of the m. pubo-ischio-femoralis internus probably originated from the internal surfaces of the ventral margin of the ilium and dorsal margin of the ischium. It may also have attached to the ventral portions of the sacral ribs, as it does in *Alligator*. This muscle would then have extended anteriorly to insert on the femur, postero-medially to the insertion of its counterpart. A shallow depression on the femur of *Orthosuchus* at this point supports this conclusion. In life the m. pubo-ischio-femoralis internus would have been a powerful muscle drawing the femur inward, upward and forward.

Ventral muscles of the hind-limb

In view of the marked development of the dorsal musculature in *Orthosuchus*, it is clear that a corresponding development in ventral musculature must have existed, as it does in *Alligator*. In the latter, the superficial layer of muscles flexing the knee consists of six muscles which unite into two groups at their insertion on the tibia.

Romer has demonstrated that in *Alligator* the external group of muscles is composed of the m. pubo-ischio-tibialis and two parts of the m. flexor tibialis internus. In lizards the m. pubo-ischio-tibialis arises along the entire ventral margin of the girdle, but in crocodiles it is confined to a small area on the lower margin of the anterior process of the proximal ischium. Since this process is more

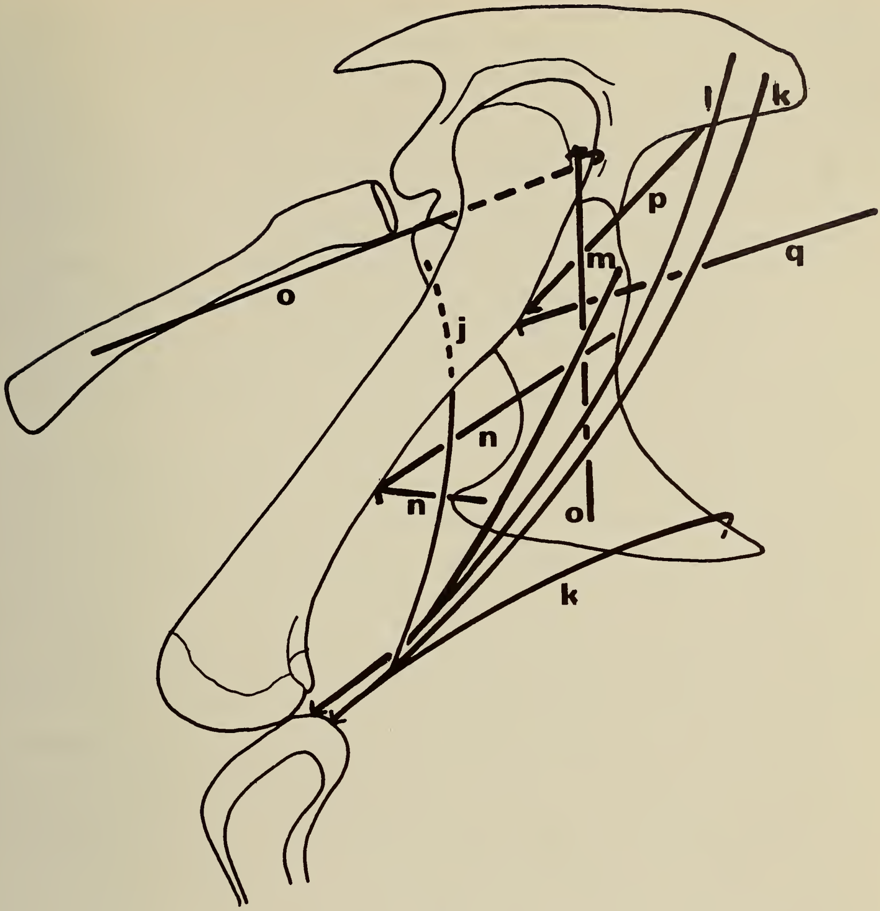

Fig. 24. *Orthosuchus stormbergi.* Diagrammatic reconstruction of the inferred main lines of action of the ventral muscles of the thigh. Abbreviations as in Figure 22.

strongly developed in *Orthosuchus* than it is in living crocodiles, it may be that the muscle too was more extensive. The m. flexor tibialis internus probably originated both on the medial surface of the ischium at its postero-ventral angle and from the posterior angle of the iliac blade. As in *Alligator*, these muscles would have inserted by a common tendon on to the medial surface of the tibia, internal to other flexors of the lower leg.

The second, internal group of muscles in *Alligator* consists of the m. flexor tibialis externus and two further parts of the m. flexor tibialis internus. In *Orthosuchus* the m. flexor tibialis externus almost certainly arose behind the m. ilio-tibialis on the posterior postacetabular iliac process. The m. flexor tibialis internus commonly arises from the ilio-ischiadic ligament, and presumably also did so in *Orthosuchus*. However, there may have been a second point of origin from the posterior margin of the proximal ischium, as occurs in *Alligator*. In both *Orthosuchus* and *Alligator* the ischium forms a marked prominence at this point. The m. flexor tibialis externus, together with the m. flexor tibialis internus, would have inserted medially on the head of the tibia. In addition, a second tendon may have passed down to unite with the m. gastrocnemius near the foot, as it does in living crocodiles.

Since the m. pubo-tibialis has been lost in both living crocodiles and birds, it seems reasonable to assume that this muscle was also absent in *Orthosuchus*.

A m. adductor femoris probably arose both below the m. flexor tibialis internus on the posterior margin of the ischium, and also from the antero-ventral angle of the blade of the ischium. This muscle would have inserted on the posterior (= ventral of Romer) surface of the femur.

The deepest muscle of the ventral musculature, the m. pubo-ischio-femoralis externus, is a powerful muscle which no doubt had much the same arrangement in *Orthosuchus* as it has in *Alligator*. In the latter, one part arises from the main area of the blade of the ischium between the two adductors, a second from the ventro-lateral surface of the pubis, and a third from the dorso-medial surface of the pubis and adjacent gastralia. These parts unite and insert on the postero-lateral margin of the femur close to its head. The femur of *Orthosuchus* bears a marked rugosity at this point, and there can be little doubt that this represents the insertion area of this muscle.

Muscles connecting the femur to the tail, which made possible a backward and downward pull on the femur, were also well developed in *Orthosuchus*. The m. coccygeo-femoralis brevis (= caudifemoralis of Gadow) almost certainly arose from the last sacral and first caudal vertebrae, and attached to the ventral surface of the posterior process of the ilium. In *Orthosuchus* this process is stouter than it is in *Alligator*, and possibly the iliac slip of the muscle was more important than the caudal. This muscle would have inserted on the femur above the fourth trochanter.

Since the fourth trochanter is relatively less well developed in *Orthosuchus* than it is in *Alligator*, a weaker m. coccygeo-femoralis longus (= caudi femoralis of Gadow) than that of recent types is indicated. This muscle would have originated on the ventral surfaces of the caudal vertebrae and inserted both on the fourth trochanter and on to the fibula.

The muscles of the lower hind-limb

A comprehensive account of the musculature of the lower hind-limb of living crocodiles was given by Von Wettstein (1937), who followed the work of Gadow (1882).

Since the form of the lower hind-limb of *Orthosuchus* is closely comparable to that of living crocodiles, there seems little doubt that its musculature also followed a similar pattern. The common extensor of the digits, the m. extensor digitorum communis, would have originated on the lateral femoral condyle and inserted on to the bases of the metatarsals. In *Alligator* this muscle unites with the m. tibialis anterior, which arises on the proximal part of the tibia, and there is a common insertion on to the four long metatarsals. This differs from the pattern found in lizards, where the two muscles remain separate. Presumably in *Orthosuchus* these muscles had an arrangement similar to that found in *Alligator*.

In crocodiles, unlike *Sphenodon*, the m. extensor peroneus brevis (anterior) and the m. extensor peroneus longus (posterior) are separate. The m. peroneus brevis arises on the fibula and inserts on the dorsal and lateral surfaces of metatarsal five, and on the dorso-lateral surface of the calcaneum. The calcaneum of *Orthosuchus* shows a shallow depression at this point, and the fifth metatarsal bears a rugosity. It therefore seems likely that in *Orthosuchus* the m. peroneus brevis had a similar relationship and, as in living genera, a comparable function of dorsiflexing the foot and elevating its lateral border. In *Alligator* the m. peroneus longus arises on the lateral condyle of the femur and inserts on to the calcaneal tuber, so that it functions to flex the lower limb. Since the tuber is strongly developed in *Orthosuchus*, there can be little doubt that this muscle had an arrangement and function comparable to that in living crocodiles.

Similarly, the m. abductor and extensor hallucis was probably as well developed in *Orthosuchus* as it is in *Alligator*. It would have originated on the distal end of the fibula and from the calcaneum, and then crossed the dorsal surface of the foot to insert on the first metatarsal.

The main flexor of the lower limb, the m. gastrocnemius, is superficial in position and has two areas of origin. In *Orthosuchus* one part would have attached to the lateral condyle of the femur, and the second to the tibia, as in *Alligator*. Further, since the calcaneum of *Orthosuchus* is strikingly similar to that of living crocodiles, there can be little doubt that this muscle had a similar insertion. One part of the m. gastrocnemius would have run from the femur to the calcaneal tuber, partly inserting on its upper surface and forming a stout tendon which ran down the vertical groove to insert on the plantar aponeurosis. The second part of the m. gastrocnemius must have inserted entirely on the tuber. In life this muscle effected flexion of the foot during the propulsive effort.

The arrangement of the m. flexor digitorum longus (= flexor primordialis communis of Von Wettstein) in crocodiles is similar to that found in other reptiles. In *Orthosuchus* it very probably had several heads of origin, principally from the lateral condyle of the femur and proximal fibula. These would have united and run medially to the calcaneal tuber to the plantar aponeurosis, finally forming tendons inserting on the distal phalanges.

In living crocodiles the m. popliteus (= tibialis posticus of Gadow) is a powerful muscle which arises from the fibula and tibia, and distally forms a tendon which passes over a groove on the astragalus to insert on to the bases of metatarsals one and two. There is no reason to suppose that a similar arrangement did not exist in *Orthosuchus*. Presumably, too, the m. pronator profundus arose on the proximal part of the tibia and inserted on to the fibula. In living crocodiles, according to Von Wettstein, the distal part of this muscle, the m. interosseus, is absent.

AGE VARIATIONS IN THE SKULLS OF RECENT CROCODILIA AND AN ANALYSIS OF THE DIFFERENCES BETWEEN THE SKULLS OF THE TYPE, K409, AND K4639

The overall skull plan in K4639 compares well with that seen in the type, K409. The skull elements of the smaller specimen also have the same relationship to one another that they have in the type. On the other hand, certain differences are also apparent. Skull dimensions are dissimilar, and in K4639 the superior temporal fenestra is oval in shape and smaller than the orbit, whereas in K409 it is more or less circular and approximates the size of the orbit.

In view of the small size and low degree of ossification of the skull elements, there can be little doubt that K4639 is a juvenile form. The lack of fusion between the parietals and lack of a squamosal ridge in this specimen could also be attributed to the juvenile condition. In K409 the parietals are fused, and there is a ridge marking the position held by ear flaps in life.

The question then is whether the differences in skull proportions can be attributed to a difference in age between individuals of a single species, or whether they are specific differences. It cannot, unfortunately, be assumed that K409 is of breeding size, though clearly it would be helpful if this point could be established.

With this in mind, some attempt to analyse the differences, and to compare these with similar dimensions in the protosuchian, *Protosuchus*, and in eusuchians, was undertaken. Mook (1921*a*) studied a series of skulls of *Crocodylus acutus* (= *Crocodilus americanus*), *Alligator mississippiensis* and *Caiman crocodilus* (= *C. sclerops*), and noticed a number of characters which could be attributed to differences in age. To supplement this a series of nine skulls of *Crocodylus porosus*, from the collection at the British Museum (Natural History), have been examined by the author.

Breadth of skulls compared with length (Fig. 25)

Mook concluded from his data that in *Crocodylus acutus* and *Caiman crocodilus* there is a marked, though irregular, broadening of the skull with age. In *Alligator mississippiensis* there is only a slight change from young to old, a slight narrowing being noticeable in older specimens.

When breadth (ordinates) and length of skulls (abscissae) are plotted against one another a somewhat curved line is obtained. If both are converted into log. form, the lines are still curved, but if log. (length) is plotted against log. (breadth–10) the lines become, for practical purposes, straight.

Regression coefficients (b) for $\log_{10}$(breadth–10) on $\log_{10}$(length) were

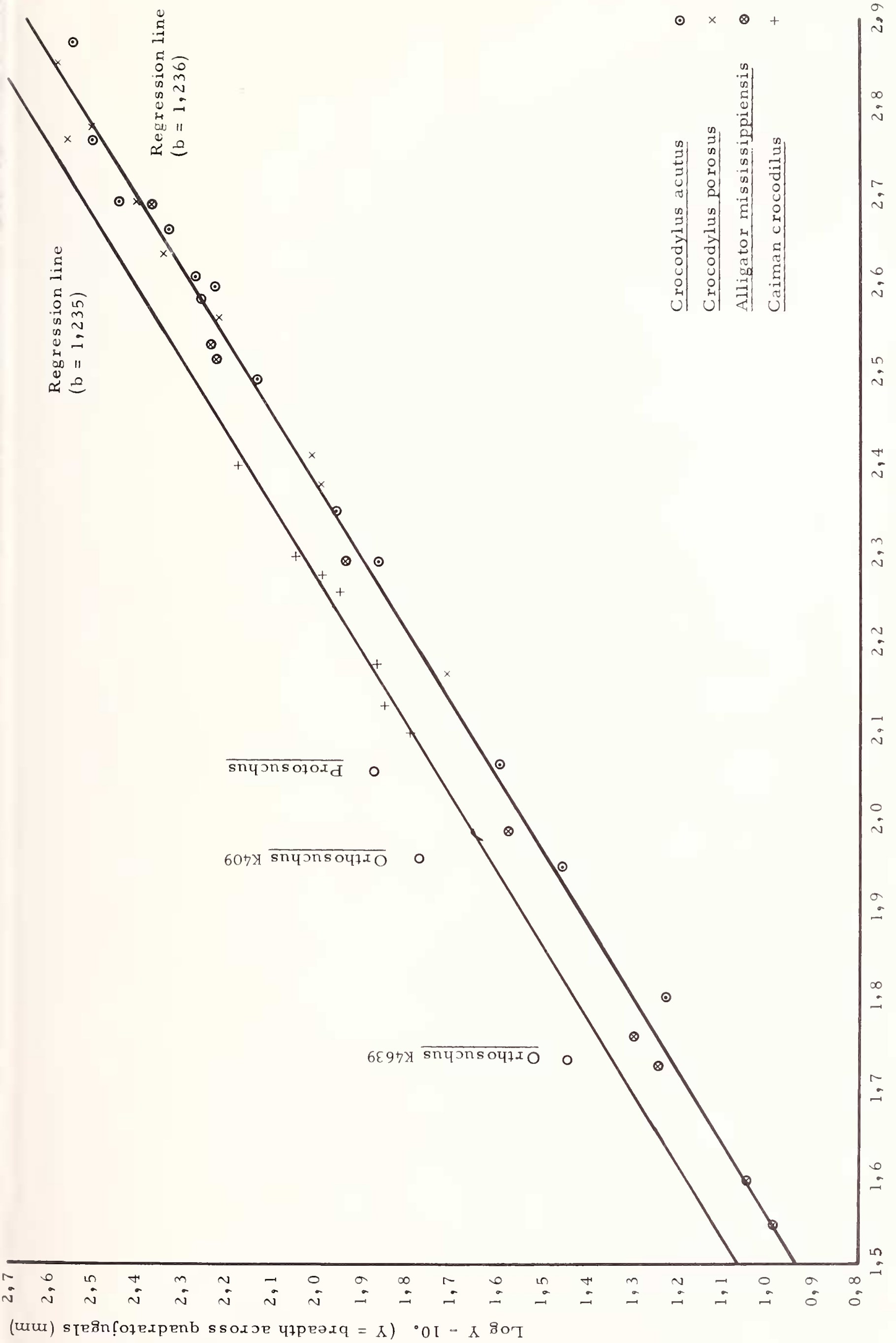

Fig. 25. Graph showing relationship between breadth and length of skull in eusuchians and protosuchians.

calculated separately for the four living species, and the following values obtained:

Caiman crocodilus b = 1,235
Alligator mississippiensis b = 1,236
Crocodylus acutus b = 1,271
Crocodylus porosus b = 1,332

The graph shows that the last three of these form a rather close group, with *Caiman* standing well outside. In the close group, the regression coefficients of *Crocodylus porosus* and of *Alligator* are the most distinct, but a *t* test shows that the difference between these coefficients is not significant (t = 1,950 with 14 d.f.).

While the position of the line for *Alligator* is perhaps marginally above the other two, it seems convenient for present purposes to combine the points for these three species and calculate one regression line. This is given by: y = 1,236x—0,9207.

From this it can be shown that the ratio of breadth/length of skull has a minimum value (0,45) for animals of skull length 115 mm. In smaller and in larger animals the breadth of the skull is relatively greater.

Although the slope of the regression line for *Caiman crocodilus* (b = 1,235) is not distinct from the slope of the line (b = 1,236) for the other three combined, the regression line for *Caiman* lies clearly separated above that for the other three groups (t = 11,265 with 34 d.f.). Thus *Caiman crocodilus* is demonstrated as a species with a relatively broader skull.

Compared with this, there is no doubt that *Orthosuchus* (K409 and K4639) and *Protosuchus* have broader skulls than living species. The values for K409 and K4639 fall together reasonably well, and the value for *Protosuchus* is in close conformity with these.

Relative size of the cranial table (Figs 26–27)

Mook (1921*a*) established that the cranial table is relatively broader in young individuals than in older ones. He related the cranial table to the breadth of the skull across the quadratojugals. The ratios of breadth of cranial table/breadth of skull in *Orthosuchus* are:

K409 = 0,78
K4639 = 0,87

These ratios compare favourably with those Mook obtained for *Alligator* and suggest that a similar growth pattern occurred in *Orthosuchus*.

It can also be seen from the data that within a species the relationship approximates to a direct proportionality between breadth of cranial table and length of skull.

The estimated ratios (from the graphs) are approximately:

Crocodylus porosus = 0,26
Crocodylus acutus = 0,27 (Fig. 26)
Alligator mississippiensis = 0,28
Caiman crocodilus = 0,35 (Fig. 27)

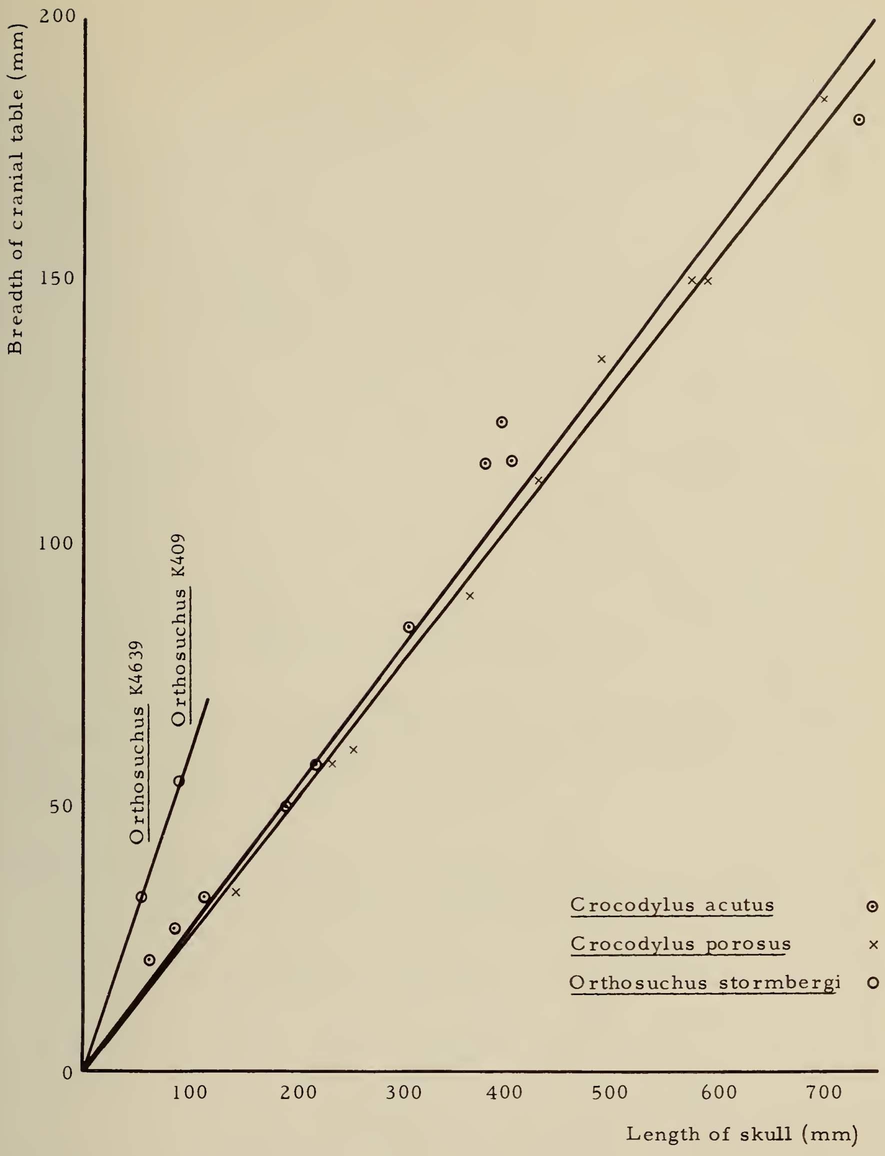

Fig. 26. Graph showing relationship between breadth of cranial table and length of skull in *Crocodylus acutus*, *C. porosus* and *Orthosuchus stormbergi*.

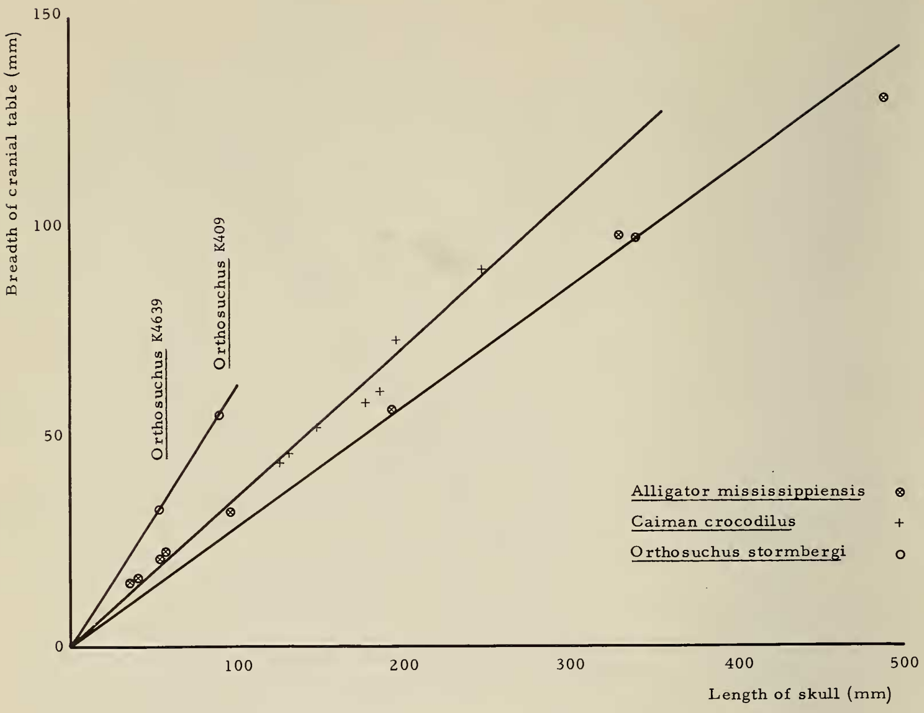

Fig. 27. Graph showing relationship between breadth of cranial table and length of skull in *Alligator mississippiensis*, *Caiman crocodilus* and *Orthosuchus stormbergi.*

Against these *Orthosuchus* shows a much higher ratio: 0,62 for both K409 and K4639.

These figures clearly separate *Orthosuchus* from the eusuchians and also show a close relationship between K409 and K4639.

Relation of preorbital to postorbital length (Fig. 28)

Mook's work on modern species showed a progressive increase in the length of the facial region as compared with the cranial region during growth. The degree to which this occurs depends on the form of the adult.

The ratios of postorbital over preorbital length for *Orthosuchus* are:

K409 = 0,96
K4639 = 1,16

These values compare favourably with those Mook obtained for brevirostrate forms, in particular that of *Caiman*. On the other hand *Protosuchus* is shown

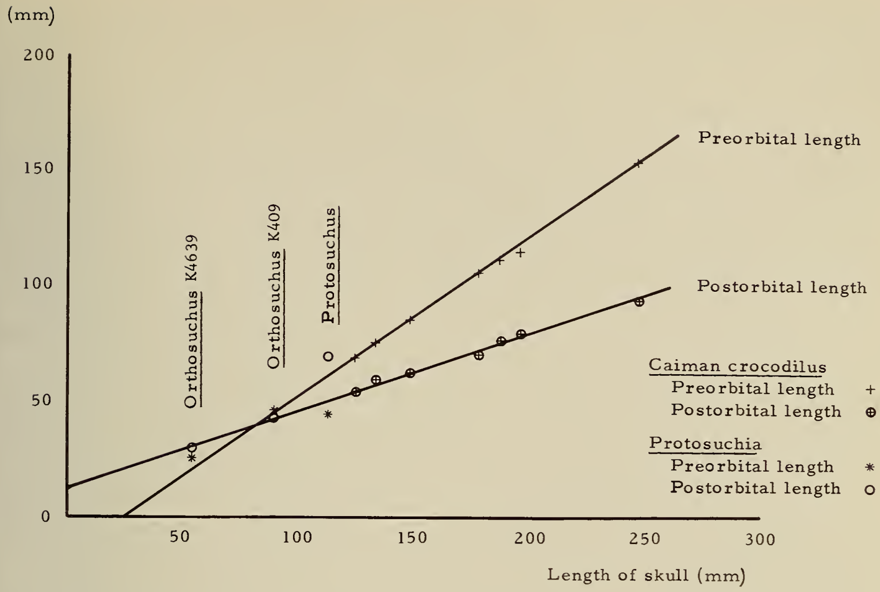

Fig. 28. Graph showing relationship between preorbital and postorbital length in *Caiman crocodilus*, *Orthosuchus* and *Protosuchus*.

to have a surprisingly short preorbital region, even assuming that Colbert & Mook (1951) made no allowance for the damaged tip. *Protosuchus* could perhaps be regarded as a juvenile of a species very much larger than *Orthosuchus*. However, both types seem to be young animals.

Relative size of the orbits (Fig. 29)

Mook noticed that the orbits of young crocodilians are relatively much larger than in full-grown animals, and expressed this as a ratio of length of orbit/length of skull. Further, he pointed out that there is a progressive increase in the relative breadth of the interorbital plate.

When the values for *Orthosuchus* K409 and K4639 are seen against those for *Crocodylus acutus* they again fall together reasonably well. In other words, the relatively longer orbits and the narrower interorbital plate of K4639, as compared with K409, could be attributed to a size (i.e. age) difference.

Although the values for *Orthosuchus* correspond closely to those for *Crocodylus acutus*, compared to both *Alligator* and *Caiman* the orbits of *Orthosuchus* are short relative to skull length. On the other hand, the interorbital region is broader in *Orthosuchus* than it is in any of these living species of a comparable size.

Relative proportions and position of the superior temporal fenestrae

Mook suggested that as a general rule, in the very young stages the superior temporal fenestrae are small and slit-like, that in later stages they

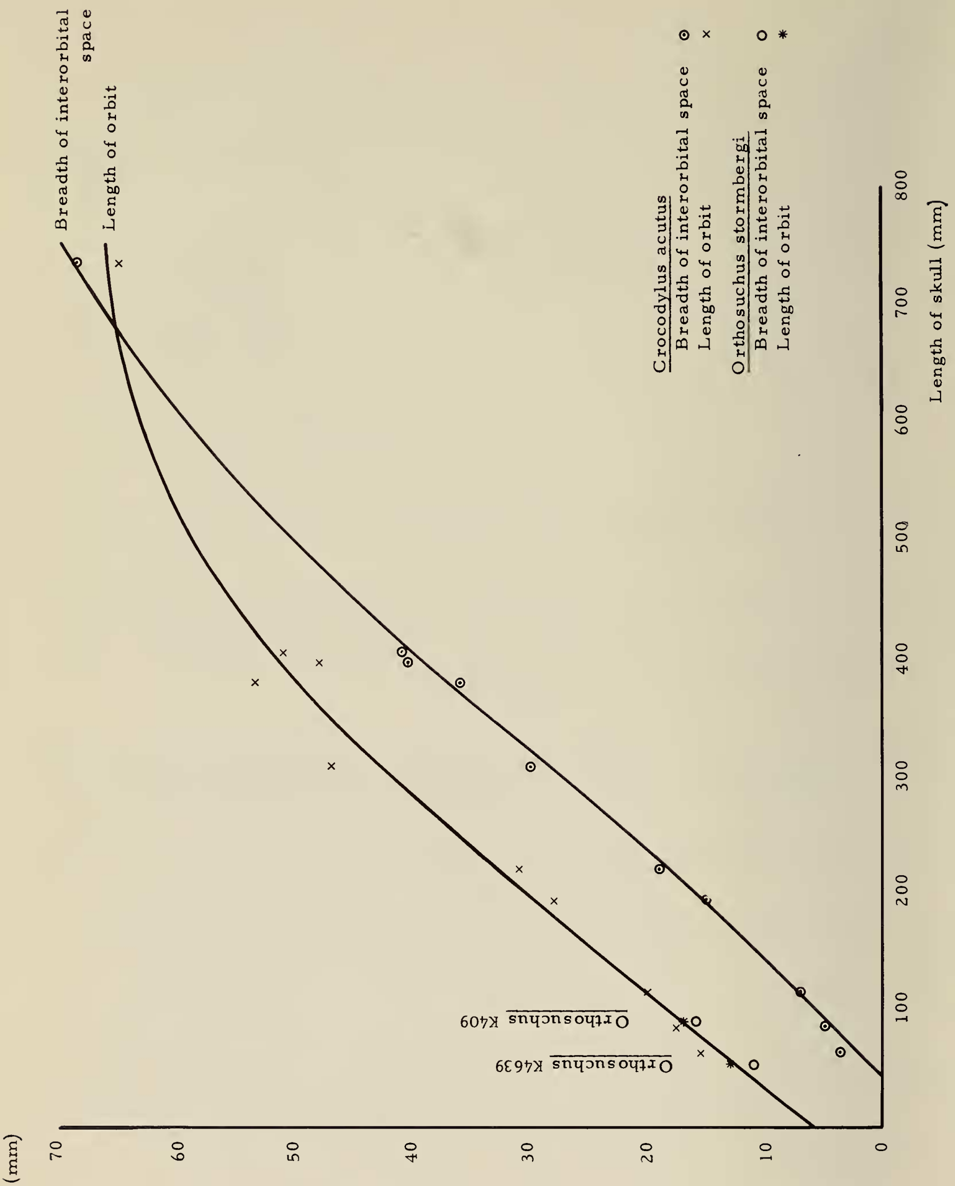

Fig. 29. Graph showing relationship between length of orbit and breadth of interorbital space n *Crocodylus acutus* and *Orthosuchus stormbergi.*

become rounder, and in old animals they usually become small and nearly circular. That the size and shape of the fenestrae are definitely size (i.e. age) related characters for the majority of species seems unquestionable. However, the precise pattern of development varies from species to species.

Mook notes that in young specimens of *Caiman crocodilus* the fenestrae are relatively large, and that in older ones they are smaller and may even eventually close at the surface. Skulls of *Crocodylus porosus* (British Museum (Natural History)) indicate that in this species the fenestrae are, in the early stages, elongate in the longitudinal direction, but when the skull reaches 300 to 400 mm in length they become round, only to elongate in the same longitudinal direction in larger specimens (Table 3).

To some extent the very elongate shape of the superior temporal fenestrae in K4639 may be due to lateral compression of the skull during preservation. However, even without this consideration it is still possible that this is a juvenile character in *Orthosuchus*, the fenestrae becoming broader and assuming a more or less circular shape in later stages. It is, of course, impossible to say whether they would have remained large, as they do in *Gavialis*, or whether they would eventually have become smaller, relative to skull size, as in other living crocodiles.

Mook also noticed that in crocodiles other than *Caiman* the superior temporal fenestrae appear to migrate inwards during growth, due to failure of growth of the intertemporal region. Hence in young specimens the centres of the superior temporal fenestrae are immediately posterior to the centres of the orbits, while in older individuals the centres of the fenestrae are posterior to the inner part of the orbits. Again, the series of skulls of *Crocodylus porosus* suggests that growth between the superior temporal fenestrae is minimal compared with increase in length and breadth of the skull, in the early stages. However, there is some evidence of a reversal of this position in skulls over 450 to 500 mm in length.

In *Orthosuchus*, despite the fact that K409 is almost twice as long as K4639, the width of the intertemporal region is the same for the two skulls (i.e. 6 mm).

On balance therefore, there seem to be no strong reasons indicating the separation of K409 and K4639. In view of the similarity of skull plan and relationship of individual elements, it seems more likely that the differences are attributable to size (i.e. age) variation. Whether K409 is juvenile, or of breeding size, is indeterminable. Much of the evidence seems to indicate that it is a young animal.

MODE OF LIFE

Orthosuchus was rather lizard-like in body proportions. The type specimen measures about two-thirds of a metre in length, and although this may well have been a young animal, other known Triassic protosuchians are all more or less the same size. The slender jaws and feeble dentition are clearly not those of a voracious predator, and on land it would have had a number of formidable competitors.

Table 3

Skull proportions in *Orthosuchus*, and *Crocodylus porosus* in mm

	Orthosuchus		*Crocodylus porosus*								
	SAM–K4639	K409	B.M.(N.H.) No. b.b.b.	1932 7.19.1.	1929 2.22.5	86.5.20.3	67.4.2.188	89.5.13.13	65.8.22.1	1902 12.19.1	47.3.5.33
Length of skull, front of snout to parietal/supra-occipital suture	54,0	90,0	145,0	235,0	255,0	365,0	430,0	490,0	575,0	590,0	700,0
Breadth of skull across external margin of quadratojugals	38,0	70,7	62,0	110,0	115,0	180,0	234,0	270,0	380,0	335,0	400,0
Breadth of cranial table at mid-level of superior temporal fenestrae	33,0	55,0	34,0	58,0	61,0	90,0	112,0	135,0	150,0	150,0	185,0
Intertemporal width	6,0	6,0	8,0	10,0	10,0	14,0	17,0	18,0	18,0	25,0	30,0
Length of superior temporal fenestra	10,0	19,0	12,0	20,0	17,0	20,0	30,0	30,0	45,0	50,0	55,0
Breadth of superior temporal fenestra	5,0	17,0	8,0	18,0	18,0	22,0	27,0	35,0	40,0	35,0	35,0
Breadth of skull/length of skull	0,70	0,79	0,43	0,47	0,45	0,49	0,54	0,55	0,66	0,57	0,57
Breadth of cranial table/breadth of skull	0,87	0,78	0,55	0,53	0,53	0,50	0,48	0,50	0,40	0,45	0,46
Breadth of superior temporal fenestra/length of superior temporal fenestra	0,50	0,89	0,67	0,90	1,06	1,1	0,90	1,17	0,89	0,70	0,64
Intertemporal width/breadth of skull	0,18	0,08	0,13	0,09	0,09	0,08	0,07	0,07	0,05	0,07	0,08

The Triassic was a time of dramatic faunal changes, with the earlier types, which were predominantly therapsids, being gradually replaced, mainly by archosaurs. Unquestionably, the dominant forms of the Upper Triassic lay among the saurischian dinosaurs. These were prosauropods of generally large size, and included both herbivorous forms like *Thecodontosaurus* and *Plateosaurus*, and carnivores like *Melanorosaurus*. It is now quite clear that the earliest known ornithischians also occurred at this time, as shown by *Fabrosaurus*, *Heterodontosaurus* and *Lycorhinus*. Thecodontians also occur in the earlier Triassic of South Africa, and *Sphenosuchus* is known from the Red Beds.

Although the mammal-like reptiles were reduced to a few genera, advanced ictidosaurs, *Tritylodon* in particular, are characteristic of the Upper Triassic. The earliest known mammal, *Erythrotherium*, is also known from these beds of South Africa. Elsewhere in the late Triassic procolophonids are present, labyrinthodont amphibians are found in Australia, and rhynchosaurs in Nova Scotia, Scotland and India.

At the end of the Triassic the large pseudosuchians and many of the prosauropods disappeared. However, the crocodiles flourished through the Jurassic, at least in a chiefly aquatic environment, as evidenced by large teleosaurs like *Mystriosaurus* and *Steneosaurus*, and highly specialized marine forms like *Metriorhynchus*.

Coupled with the change in fauna there was, at least in South Africa (Haughton 1924), a progressive increase in aridity from the Lower through to the Upper Triassic. Yet, however tempting it may be to suppose that *Orthosuchus* was essentially terrestrial in habit, there are undeniable indications that it spent much of its time in water, as do living crocodiles.

This is most clearly shown by the form of the palate. Although *Orthosuchus* has only a short secondary palate, the form of the vomers and palatines and ridging on the pterygoids leave little doubt that a functional secondary palate extended well back to the base of the skull, as in living crocodiles. The palate of *Orthosuchus* differs only in that it was floored by soft tissue rather than by bone. Hence in *Orthosuchus* the functional choanae opened well back, and conceivably a valve apparatus was present which sealed off the glottis when the mouth was open. *Orthosuchus* was probably able to remain submerged, leaving only the external nares open above water to act as a snorkling device.

Ear flaps may also have evolved to prevent flooding of the otic region. Shute & Bellairs (1955) have shown that modern crocodiles close the ear-flaps when they submerge, though this action does not necessarily prevent water from entering the recess. It is difficult to see why ear flaps would have been developed for a terrestrial habit, when their closure in modern species reduces conduction of aerial sound to the ear by 10 to 12 db over most of a frequency range of 100 to 6 000 cycles (Wever & Vernon 1957).

Amongst living crocodiles the overall skull shape of *Orthosuchus* is paralleled most closely by that of the Indian gharial, *Gavialis gangeticus*. In both forms the snout is very slender and set off sharply from the skull table, though in *Gavialis* the snout is very much more elongate than it is in *Orthosuchus*. *Gavialis* feeds primarily on small fish. An individual will creep towards a shoal of fish, and then remain motionless whilst snapping sideways at the prey. The skull shape of *Orthosuchus* is possibly an adaptation for this kind of aquatic predation.

Most probably *Orthosuchus* spent much of its time in lakes or swamps, and this mode of life would have afforded certain advantages. Food in the form of small fishes and aquatic invertebrates would have been plentiful and more easily obtainable than a comparable diet on land, while the water would have provided an admirable escape route from terrestrial predators.

Ewer (1965) came to the conclusion that the antorbital fenestra in *Euparkeria* housed a gland, suggesting that this might have been a salt gland. The nature of the fenestra in *Orthosuchus* also strongly indicates that in life it housed a gland, whose secretion would have passed through a duct occupying the groove leading to the lower orbital margin.

However, whereas thecodontians like *Euparkeria* typically have a large antorbital fenestra, it decreases in relative size through *Orthosuchus* to early aquatic mesosuchians like *Teleosaurus*, is nearly always absent in highly specialized marine forms like *Metriorhynchus* and *Geosaurus* and is lost in living crocodiles. Presumably therefore the gland was more important in terrestrial than in marine forms.

In contrast, a salt-secreting gland is predominantly important in marine animals. Salt secretion by marine turtles is particularly well known, and occurs from one of the orbital glands. Among other reptiles salt secretion is known to occur from the nasal gland in lizards. Although some terrestrial forms, such as the tropical lizard, *Iguana iguana*, and the American desert lizard, *Dipsosaurus dorsalis*, secrete significant quantities of salt, they do not do so in the large amounts found in their marine relatives (Schmidt-Nielsen 1963). Birds also possess a salt-secreting nasal gland, which is normally located in the orbit. Again, in terrestrial forms it is very small, but is large in marine species. Indeed, to some extent its size varies with exposure to salt loads.

Unfortunately, almost no work has been carried out in this field on crocodiles. Schmidt-Nielsen (1960) found that a single specimen of the estuarine crocodile, *Crocodylus porosus*, did not respond to osmotic loads. This is the most thoroughly aquatic and frequently marine species of all living crocodiles.

In living crocodiles a well-developed nasal gland lies anterior to the preconcha, with its duct running anteriorly. Both a lachrymal and a large Harderian gland lie within the orbit. The antorbital gland of *Orthosuchus* was possibly an additional orbital gland, and the patches of glandular tissue which occur on the conjunctiva of the lower lid in *Crocodylus porosus* may represent the vestige of this gland.

Taking fore- and hind-limb lengths as humerus + radius + radiale, and femur + tibia respectively, the length of the fore-limb approximates that of the hind-limb in both *Orthosuchus* and contemporary crocodilians (table 4). Two large specimens of *Crocodylus niloticus* showed a fore-limb 83% and 88% the

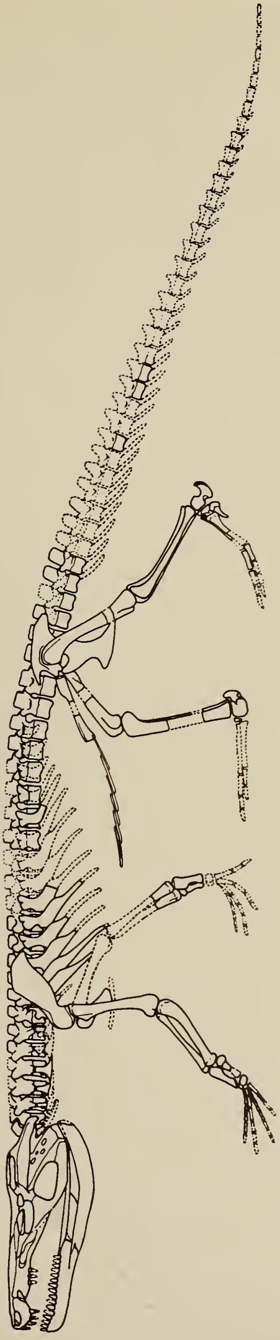

Fig. 30. *Orthosuchus stormbergi*. Restoration of the skeleton in standing pose (tail based on proportions found in living crocodiles) ($\frac{1}{4}$ natural size).

length of the hind. A smaller individual of *C. acutus* had a ratio of 98%, while in a juvenile of *Alligator mississippiensis* the ratio was 91%. Although both femora of *Orthosuchus* are now broken, the suggested measurement of 57 mm can only be a little short, if at all, of the true length. Using this measurement, the fore-limb is then 91% the length of the hind. *Orthosuchus* falls well within the range for living crocodilians and was quadrupedal (Fig. 30).

Ewer (1965) noted the significance of trunk length in determining the type of locomotion. Trunk length is taken as the distance along the vertebral column from a point directly over the pectoral glenoid to one over the acetabulum. The longer the trunk, relative to the length of the hind-limb, the more quadrupedal the type.

Of four large specimens of *Crocodylus* studied, it was found that in *C. niloticus* the hind-limb was 44% and 52% the length of the trunk, in *C. acutus* it was 49%, and in *C. porosus* 50%. In a juvenile *Alligator* the trunk is shorter relative to the length of the hind-limb, as is also the case in *Orthosuchus*, a value of 61% being obtained in both types. Ewer found a value of 40% and 50% in *Varanus* and *Sphenodon* respectively, and 70% in the fast-running quadrupedal *Agama*.

There can be little doubt that *Orthosuchus* could rest on its belly with the femur held horizontally as is the practice of modern reptiles. On the other hand, the structural features of the femur and pelvis indicate that the femur was pulled into a more nearly vertical position when the animal was moving. Living crocodiles when walking unhurriedly over land, and when hauling out of water, do so with the limbs held vertically; a movement described by Cott (1961) as the high walk. A comparison of the femur of *Orthosuchus* with that of living crocodiles shows remarkable similarity in form between the two types. However, in *Orthosuchus* the articular surface of the femoral head is more medially directed, suggesting that the femur was usually held in a vertical position. The deep acetabulum and pronounced supra-acetabular buttress would have been advantageous with the femur held in this position. The musculature essential for this type of movement was well developed.

The crurotarsal ankle joint of *Orthosuchus* is admirably suited to the action of a vertically orientated femur. By virtue of the longer length of the tibia posteriorly, it is possible for the pes to be forwardly directed while the crus passes backwards. The presence of a calcaneal tuber clearly gives greater leverage to movement of the foot. *Orthosuchus* would therefore have moved in a plantigrade manner, much as living crocodiles do when walking over land.

Although the pectoral musculature was apparently well developed, in certain respects the humerus of *Orthosuchus* is more primitive in form than that of living crocodiles. The pronounced medially directed deltopectoral crest seems to obviate any possibility of the humerus being held vertically. In this position it would foul the coracoid, on protraction at least. The humerus also shows greater twisting through its axis, so that the distal articular surface, and the lower fore-limb, must have been more laterally directed than it is in living crocodiles. On the other hand, the elongation of the radiale and ulnare appears to be a means of both lengthening the fore-limb, and providing a more flexible wrist movement, so making quadrupedal locomotion more efficient.

On rare occasions juvenile crocodiles move by galloping. Cott (1961) likens this movement to the bounding of a squirrel. In view of the more primitive posture held by the fore-limb of *Orthosuchus* it seems unlikely that the animal could have moved in this way. The lengthening of the coracoid in living crocodiles has presumably increased the length of the adductor muscles of the fore-limb, and also their efficiency.

Similarly, the tail in living crocodiles is probably used more efficiently as a propulsive organ when swimming than it was in *Orthosuchus*. The vertebrae of *Orthosuchus* are amphicoelous, whereas in eusuchians they are procoelous except for the centrum of the first caudal, which is biconvex. Further, the caudifemoral musculature was probably less well developed, as seen by the small size of the fourth trochanter. Presumably therefore the tail was less mobile than it is in living crocodiles, where it can be swung through a full circle of 360 degrees.

RELATIONSHIP OF *ORTHOSUCHUS* TO THECODONTIANS

Orthosuchus demonstrates many characters which are indicative of a thecodontian heritage. The snout is slender, as is typical of thecodontians like *Cerritosaurus* (Price 1946), and the maxilla is excluded from the boundary of paired, laterally orientated external nares. The teeth are thecodont, conical and undifferentiated.

An antorbital fenestra, bounded by the maxilla antero-ventrally and by the lachrymal postero-dorsally, is present in *Orthosuchus* as in thecodontians. Similarly, both temporal openings are well developed. The posterior margin of the inferior temporal fenestra is angular.

There is no tabular or supratemporal in *Orthosuchus*, and a postparietal is also absent. This element is known in a few thecodontians such as *Euparkeria* (Ewer 1965), but is lost in later forms. A parietal foramen is absent, as it is in the majority of thecodontians. A very tiny parietal foramen is present in certain early types such as *Chasmatosaurus* (Brink 1955) and *Erythrosuchus* (Broom 1905).

An otic notch is present in *Orthosuchus*. Although this is not developed in early thecodontians like *Chasmatosaurus* (Broili & Schröder 1934), it is generally present in later forms. In these types, as in *Orthosuchus*, the notch is open posteriorly.

In *Orthosuchus* the head of the quadrate rests in a socket of the squamosal adjacent to the paroccipital process. This is characteristic of thecodontians such as *Stagonolepis*. Similarly, a small basipterygoid process of the basisphenoid is present in *Orthosuchus*. In thecodontians such as *Chasmatosaurus* and *Euparkeria* these joints are highly developed and mobile. Case (1922) describes prominent basipterygoid processes in *Desmatosuchus spurensis* and Walker (1961) notes their presence in *Stagonolepis*, and (1964) in *Ornithosuchus*. Short basipterygoid processes allowing for some possibility of movement are also seen in phytosaurs such as *Machaeroprosopus* (Camp 1930).

In that the pterygoid is firmly applied both to the quadrate and to the basipterygoid process, it seems unlikely that the basal articulation of *Orthosuchus* was movable. Similarly, movement between the squamosal and the superior edge of the quadrate and quadratojugal seems unlikely, and the supraoccipital and parietal are firmly united. The skull of *Orthosuchus* should not therefore be regarded as kinetic, though it cannot be far removed from an ancestor with this type of skull.

In both *Desmatosuchus* and *Stagonolepis* a simple pit lies between prominent basipterygoid processes in exactly the same position as in *Orthosuchus*. It therefore seems probable that the median eustachian system of the Crocodilia does not correspond to the spiracular gill slit, but is a secondary formation developed as an intucking of the basisphenoid.

The lower jaw of *Orthosuchus* is slender with a very large external mandibular fenestra. This is characteristic of thecodontians, with the exception of primitive forms such as *Chasmatosaurus* and *Erythrosuchus*. The internal adductor fossa is also large.

Thecodontians show a range in the count of presacral vertebrae. *Euparkeria* has 22, while both *Vjuskovia* (Von Huene 1960) and *Stagonolepis* have 25. In *Orthosuchus* the number is probably 24. There are seven cervicals in *Euparkeria*, while the probable number in *Orthosuchus* is eight. The centra are amphicoelous in each case.

Behind the axis, the cervical vertebrae of both *Orthosuchus* and thecodontians like *Euparkeria* and *Ornithosuchus* show strong ventral keeling, and hypapophyses are not developed. The dorsal vertebrae, however, are not keeled.

The areas of attachment for the cervical ribs of *Orthosuchus* are distinctive and show the same progressive change in rib articulations that occurs in archosaurs generally. The parapophysis of the anterior cervical vertebra lies antero-ventrally on the centrum. Above this the diapophysis lies anteriorly, low down on the neural arch. Back through the cervicals the parapophysis moves up the centrum, while the diapophysis rises and moves posteriorly so that at the end of the series it is borne on a transverse process.

The migration of the parapophysis continues through to the dorsals, where early on it comes to lie wholly above the neurocentral suture. In *Euparkeria* it reaches this position on vertebra fourteen (i.e. dorsal six), in the phytosaur *Machaeroprosopus* on vertebra twelve (i.e. dorsal five) and in *Stagonolepis* on vertebra ten (i.e. dorsal one). In *Orthosuchus* this occurs on vertebra twelve (i.e. dorsal four). The diapophysis does not change its position further back in the series, though the parapophysis continues to move upwards until the two facets come to lie at the same level on the posterior dorsals. They become confluent on the last presacral. This can be seen in *Chasmatosaurus* and *Ornithosuchus*, and also occurs in *Orthosuchus*. In many thecodontians, such as

Euparkeria and *Chasmatosaurus*, the transverse processes become shorter from the mid-dorsal vertebrae back to the sacrals, as they do in *Orthosuchus*. In others, such as *Stagonolepis* and *Parringtonia* (Von Huene 1939), they remain the same size.

The sacral vertebrae of *Orthosuchus* are very similar to those of many thecodontians. *Orthosuchus* has retained the primitive count of two sacrals, as found in various thecodontians, including *Erythrosuchus*, *Aëtosaurus* (Walker 1961) and *Ticinosuchus* (Krebs 1963*a*). In other thecodontians, however, the number of sacrals has been increased. In *Ornithosuchus* there are three, and in *Schleromochlus* (Woodward 1907) there are four.

Atlantal and axial ribs are poorly known in thecodontians, but in some types at least, as in *Euparkeria* and *Chasmatosaurus*, they are single-headed, as in *Orthosuchus*. Other cervical ribs of *Orthosuchus* have a shape which is typical of both thecodontians and crocodilians. That is, the blade of the rib is directed antero-posteriorly with two heads rising vertically from a point along the length of the shaft. The length of the shaft is variable. It is long and slender relative to the length of the cervical vertebra in *Chasmatosaurus*, but it is short in *Orthosuchus*, as it is in the unrelated phytosaurs.

In both thecodontians and crocodilians the cervical ribs grade into the quite different form of dorsal rib. Coupled with the change which occurs in the position of the rib facets, the capitulum becomes terminal on the rib shaft, and the tubercle gradually approaches this. In *Orthosuchus* the two processes remain distinct throughout the major part of the dorsal series. A similar condition occurs in *Euparkeria*.

The scapula of *Orthosuchus* is similar to that of *Stagonolepis* and *Euparkeria* in that it is a tall, narrow element expanded at both its upper and lower ends. In many of the less specialized lepidosaurs like *Sphenodon* the scapula is relatively short and broad.

The humerus is long and slender in *Orthosuchus* as in thecodontians generally, as shown by *Hesperosuchus* (Colbert 1952) and *Ornithosuchus*. It further resembles that of thecodontians like *Euparkeria* and differs from lepidosaurs in that distally the two condyles are well apart, and the ectepicondylar and entepicondylar expansions are slight.

In *Orthosuchus* as in all archosaurs, the ulna is stouter than the radius. Further, there is no development of an olecranon process, and the head of the ulna is expanded for weight support. In thecodontians generally there is little or no development of an olecranon, though Walker (1961) notes its presence in *Stagonolepis*.

The ilium of *Orthosuchus* is, in general form, persistently primitive. As in *Erythrosuchus* and *Machaeroprosopus* it has a low iliac blade with a well-developed posterior extension. There is also a pronounced supra-acetabular buttress overhanging the acetabulum.

In the presence of a fourth trochanter and absence of a greater trochanter, the femur of *Orthosuchus* closely resembles that of thecodontians. Ewer describes the fourth trochanter of *Euparkeria* as lying well down the shaft, but in both *Orthosuchus* and *Stagonolepis* it arises about one-third of the way down.

The ankle joint of *Orthosuchus* is of crurotarsal type, a feature which has been considered of diagnostic significance for the Crocodilia. Yet, as Krebs (1963*b*) has shown, the crurotarsal ankle joint is common to all but a few pseudosuchians of Lower and Middle Triassic age. *Euparkeria* has the crurotarsal type of ankle joint, though it lacks the elaborate articulation between the astragalus and calcaneum that is found in crocodiles. The ankle joints of *Aëtosaurus* and *Typothorax* are also crurotarsal (Walker 1961). In these forms, as in *Orthosuchus*, two distal tarsals are present. A pronounced tuber is present on the posterior face of the calcaneum of *Orthosuchus*, and this too occurs in some thecodontians, such as *Saltoposuchus* (Von Huene 1921) and *Aëtosaurus*.

Thecodontians in general show some reduction of the fifth digit. In *Euparkeria* the fifth metatarsal is somewhat hooked in shape, and bears three shortened phalanges. In *Aëtosaurus* the fifth digit is more or less similar to this but bears four phalanges. In *Orthosuchus* this metatarsal is further reduced and phalanges are lacking. The pseudosuchian *Schleromochlus* apparently shows a condition identical to that seen in *Orthosuchus*.

Orthosuchus was protected dorsally throughout its length by a paired row of bony plates. Many thecodontians show a similar development of armour. *Ornithosuchus* has, as far as is known, only dorsal armour, the scutes being arranged in a paired, longitudinal series. *Ticinosuchus* and *Euparkeria* have both dorsal and lateral scutes, while *Stagonolepis* was protected at least in part on its ventral surface as well. *Ornithosuchus* and *Stagonolepis* also show the same bending down of the outer portions of the scutes at right angles to the dorsal portions, as seen in *Orthosuchus*. Furthermore, the characteristic peg and socket articulations between adjacent scutes in *Orthosuchus* also occurs in both *Stagonolepis* and *Ornithosuchus*.

Gastralia are present in *Orthosuchus*, as they are in thecodontians such as *Euparkeria*, *Ticinosuchus*, *Stagonolepis*, *Schleromochlus* and *Rutiodon* (McGregor 1906).

RELATIONSHIP OF *ORTHOSUCHUS* TO CROCODILIANS

There are few unquestionable crocodilians of Upper Triassic age. *Protosuchus richardsoni* from Arizona is the best known of these. The type described by Colbert & Mook (1951) is a nearly complete, articulated skeleton. Seven other partial skeletons were also collected from the same locality and stratigraphic level.

Two partial skeletons of *Notochampsa istedana* are known. The type described by Broom (1904) from the Cape Province is an impression of the nasal and temporal regions of the skull, a good pectoral girdle and fore-limb, part of the hind-limb and dorsal armour. The other specimen, British Museum (Natural History) No. R8503, as yet undescribed, is from Lesotho and consists

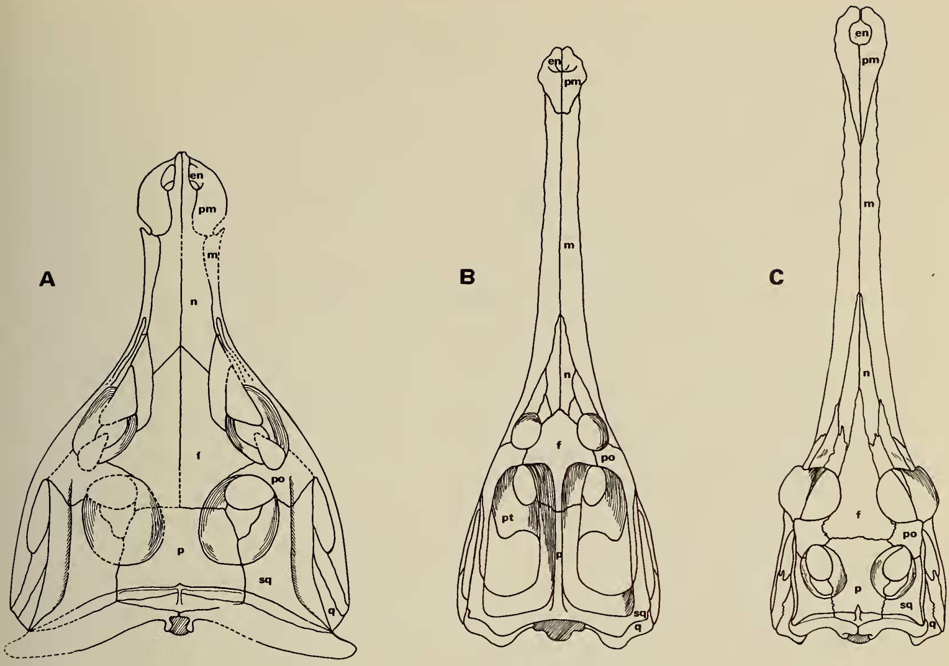

Fig. 31. Dorsal views of the skulls of A. *Orthosuchus stormbergi* ($\frac{2}{3}$ natural size). B. *Steneosaurus durobrivensis,* after Andrews (1913*a*) ($\frac{1}{12}$ natural size). C. *Gavialis gangeticus* (juvenile).

of the left temporal region of the skull and part of a jaw ramus, a few vertebrae, some isolated limb elements and armour.

Erythrochampsa longipes is rather poorly known only from part of the postcranium and armour. The type specimen is from the Cape Province, and was described by Broom (1904). Further material from the Orange Free State was assigned to this genus by Broili & Schröder (1936).

In general form the skull of *Orthosuchus* is very similar to those of *Protosuchus* and *Notochampsa.* In all these forms the cranial table is broad and flat, and is of characteristic crocodilian shape. The snout is slender and clearly marked off from the rest of the skull, a pattern which is seen in many mesosuchians, notably teleosaurs, metriorhynchids and pholidosaurs, and one which is retained in certain eusuchians, principally *Gavialis* (Fig. 31). Further, the bones are sculptured in true crocodilian fashion in all these forms.

It seems likely that the external nares of *Orthosuchus* are similar to those of *Notochampsa.* Haughton (1924) felt that there was sufficient evidence in the nasal region to prove that they were paired and somewhat lateral. The tip of the snout of *Protosuchus* is not known, but in *Steneosaurus* (Andrews 1913*a*) the external nares are confluent. Ventrally the premaxilla of *Steneosaurus* is not extensive and differs little from that of *Orthosuchus.*

In both *Orthosuchus* and *Protosuchus* there is a short region of the snout which does not bear teeth. In *Protosuchus* this is described as being comparable to the notch region in later crocodiles, though in *Orthosuchus* a prominent notch also occurs. Behind this there are in *Orthosuchus* three or four maxillary teeth, in *Notochampsa* between six and nine, and in *Protosuchus* about eleven. Von Huene (1925) described the teeth of *Notochampsa* as not compressed and without edges, and this description is equally applicable to *Orthosuchus* and *Protosuchus.*

The orbits of *Orthosuchus* and *Protosuchus* are directed outward and forward rather than predominantly upward as in more advanced forms. There is now no doubt that Colbert & Mook (1951) interpreted the orbital region of *Protosuchus* incorrectly. They considered the orbital region to be wide, but clearly in both *Orthosuchus* and *Protosuchus* this region is relatively narrow and is bordered on either side by two supraorbital elements. Unfortunately, the orbital region of *Notochampsa* is not preserved, though in the more recent material, British Museum (Natural History) No. R8503, the anterior margin of the left postorbital bears a facet for a supraorbital element. This surely indicates that the orbit was outwardly directed as in *Orthosuchus.*

The postorbital-jugal bar in *Orthosuchus* and *Protosuchus* is superficial in position, as it is in teleosaurs. The superior part becomes sunken in metriorhynchids, pholidosaurs and notosuchids, and it is wholly displaced internally in goniopholids and atoposaurs, and in all eusuchians.

Much has been written regarding the position of the orbits of crocodiles in relation to an aquatic mode of life. It seems that the change in orientation from the more lateral position found in early crocodiles to the dorsal inclination of living forms should be attributed to the movement of the jugal upwards from an essentially horizontal position in *Orthosuchus* into a nearly vertical one. This is coupled with the inward movement of the postorbital bar. Supraorbital elements lie over the roof of the orbit in the eyelid in both modern crocodiles and *Orthosuchus.*

Despite the position of the orbits in *Orthosuchus*, there are clear indications in the form of the palate and overall shape of the skull, that the trend towards a semi-aquatic mode of life was already well established. In view of the remarkable similarity in form between the North American and southern African protosuchians, it seems that *Protosuchus* too was rather more aquatic in habit than has previously been supposed.

Differences between the protosuchians lie in the shape of the superior temporal fenestrae. *Notochampsa* is characterized by the moderately sized, almost pear-shaped superior temporal fenestra, which lies with its broadest end anteriorly. In *Protosuchus* this fenestra is circular in shape, and is smaller than the orbit, and in this respect shows an inherent thecodontian condition. In *Orthosuchus* the superior temporal fenestra is also circular, but equals the size of the orbit. This indicates a progression toward the condition shown by early mesosuchians such as *Teleosaurus* (Andrews 1913*a*) where the fenestra is greatly enlarged at the expense of the parietal and squamosal.

Kalin (1955) suggests that the enlargement of the superior temporal fenestra seen especially in long snouted groups, such as the gharial, is correlated with the form of the musculature. In those longirostrate forms adapted for fish eating there is a need for a well-developed m. adductor mandibulae externus, which arises within the superior temporal fossa. On the other hand, in brevirostrate crocodiles, where prey is held in the water to drown it, or where large animals are torn apart, it is the m. pterygoideus which is strongly developed.

Since *Orthosuchus* would appear to be more progressive than *Protosuchus* with regard to the size of the superior temporal fenestra, it is surprising that an antorbital fenestra is present in *Orthosuchus* and lacking in *Protosuchus*. Unfortunately this question remains unresolved for *Notochampsa*. Haughton (1924) omits to mention this point at all. According to Von Huene (1925) an antorbital fenestra is present in *Notochampsa*, though Broom (1927) considered it absent. In fact, the material is too incomplete for a proper determination to be made.

Among mesosuchians an antorbital fenestra is seen in teleosaurs like *Steneosaurus* and *Pelagosaurus* (Eudes-Deslongchamps 1864) and also occurs in notosuchids such as *Notosuchus* and *Araripesuchus* (De Gasparini 1971). It has previously been supposed that this represents a secondary formation, but the presence of an antorbital fenestra in *Orthosuchus* demonstrates that this is not the case. In all types the opening lies between the maxilla and lachrymal.

In *Orthosuchus* the frontal contributes to the anterior border of the superior temporal fenestra, as it does in all mesosuchians with the exception of a few notosuchids like *Notosuchus*. In view of this it seems most unlikely that the frontal is excluded from the fenestra in *Protosuchus*, as Colbert & Mook (1951) suggest. They indicate a short suture running from the medial border of the superior temporal fenestra on each side, and it seems likely that this represents the fronto-parietal suture. In eusuchians this suture is located further forward, so that the parietal articulates with the postorbital.

In both *Orthosuchus* and *Notochampsa* British Museum (Natural History) No. R8503 a deep otic recess is made between the overhanging squamosal and sloping quadrate. In each case the squamosal bears a longitudinal groove, indicating that in life the recess was concealed by ear-flaps.

As is also characteristic for the Crocodilia, in both these forms the quadrate contributes to the floored-in area of the superior temporal fossa. The relationships of the quadrates of *Notochampsa* and *Orthosuchus* are, in fact identical. In both the otic notch is shallow and the quadrate has a posterior articulation with the squamosal. Mesosuchians differ in that the notch is deepened by the loss of the posterior articulation, as seen in *Pelagosaurus*. In eusuchians the squamosal extends down to close the notch posteriorly (Fig. 32).

Notochampsa also has a highly fenestrated quadrate, though it differs from that of *Orthosuchus* in its overall pattern. A well-developed rhomboidal sinus lying behind the prootic-opisthotic suture, between the braincase and

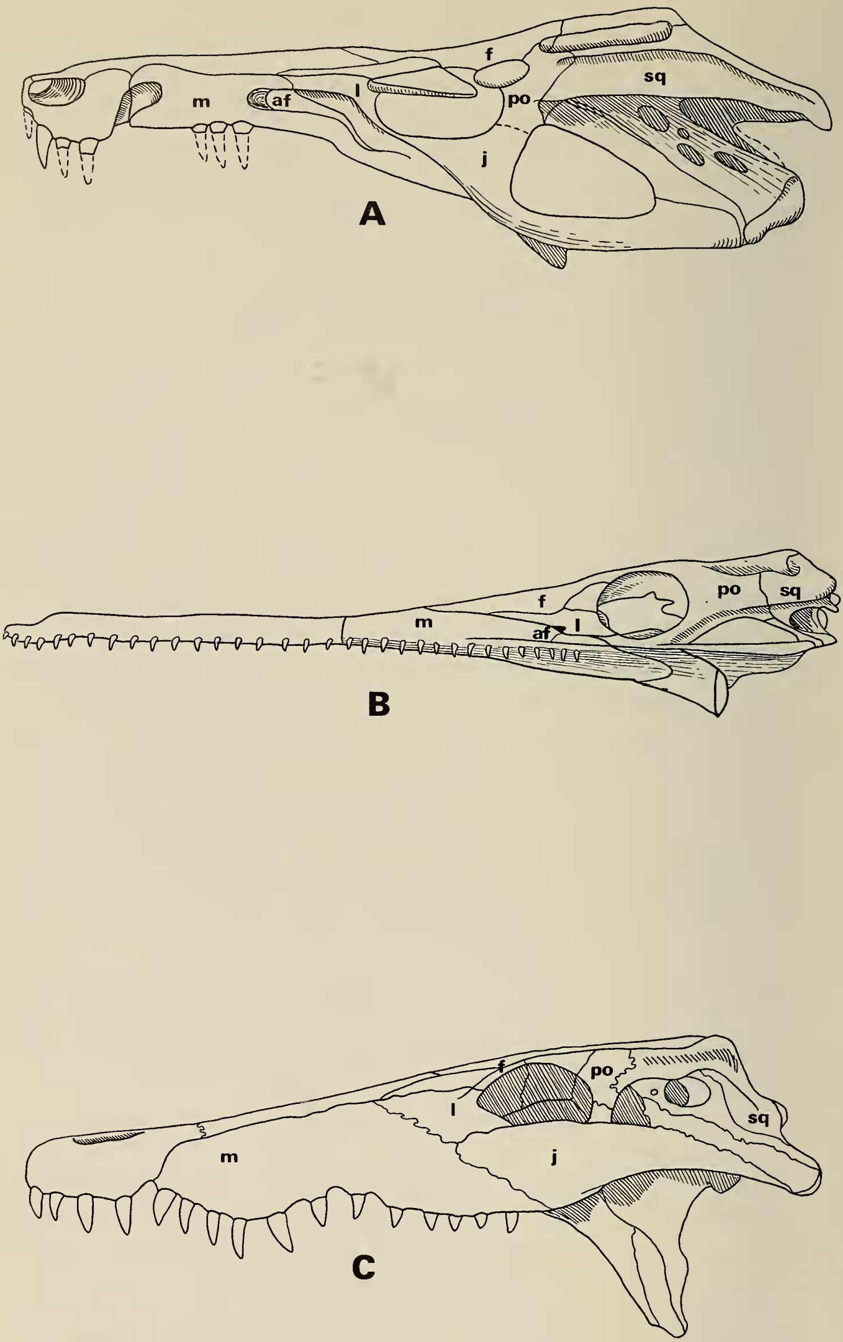

Fig. 32. Lateral views of the skulls of A. *Orthosuchus stormbergi* (natural size). B. *Pelagosaurus typus*, after Eudes-Deslongchamps (1864) ($\frac{1}{3}$ natural size). C. *Crocodylus*, after Romer (1956).

exoccipital, is present in *Notochampsa*. This clearly indicates an early stage in the enlargement of the tympanic cavity in crocodiles. The rhomboidal sinus probably opened into the throat through lateral eustachian foramina. These can be seen in *Orthosuchus*.

In living crocodiles the tympanic cavities are further enlarged and linked together by large air spaces within the supraoccipital. Each cavity is also connected to air passages within the quadrate and articular as well as to a rhomboidal sinus. This is linked to the throat by a lateral eustachian tube which passes up between the basisphenoid-basioccipital suture. In addition, a third eustachian tube passes up in the midline and divides above into an anterior and a posterior canal. Each of these forks into horizontally running canals which also terminate in the rhomboidal sinus.

This complex system of eustachian tubes is partially developed in *Pelagosaurus* and *Steneosaurus*, where the anterior branch of the median eustachian tube, with its horizontal branches, is found. Unfortunately, in *Orthosuchus* it is impossible to determine whether the comparable anterior canal also leads to a rhomboidal sinus on either side.

A very large horizontal canal connects the median and lateral eustachian foramina on each side in *Pelagosaurus* and *Steneosaurus*. These surely represent the canals of the posterior branch of the median eustachian system. These canals are not developed in *Orthosuchus*. On the other hand, in both *Orthosuchus* and *Steneosaurus* an additional canal leads backwards from the median opening and, in *Steneosaurus*, runs into the body of the basioccipital and Andrews (1913*a*) was of the opinion that this canal was vascular in function.

In mesosuchians the lateral eustachian tubes are membranous, as is the median tube, and each lateral foramen opens above directly to a rhomboidal sinus. Presumably the enclosure of these tubes by bone occurred as a result of growth of the basioccipital and basisphenoid. This, coupled with the more limited extension of the pterygoid posteriorly, must account for the apparent change in position of the eustachian foramina from the pterygoid-basisphenoid suture, as in *Orthosuchus*, to that between the basisphenoid and basioccipital, as in later crocodiles.

This complex eustachian system in crocodiles probably functions as a series of resonance chambers to improve auditory capacity. Wever & Vernon (1957) have demonstrated that because the two middle ear cavities are interconnected, the application of sounds to one ear stimulates the other ear almost equally well.

The pterygoid of *Steneosaurus* is essentially similar in form to that of *Orthosuchus* (Fig. 33). In both types it has a posterior process which extends back along the side of the basis cranii as far as the basisphenoid-basioccipital suture and makes contact with the exoccipital so that the quadrate does not meet the basisphenoid as it does in modern forms. In *Pelagosaurus* this process of the pterygoid does not extend as far back, and in modern forms only a vestige remains.

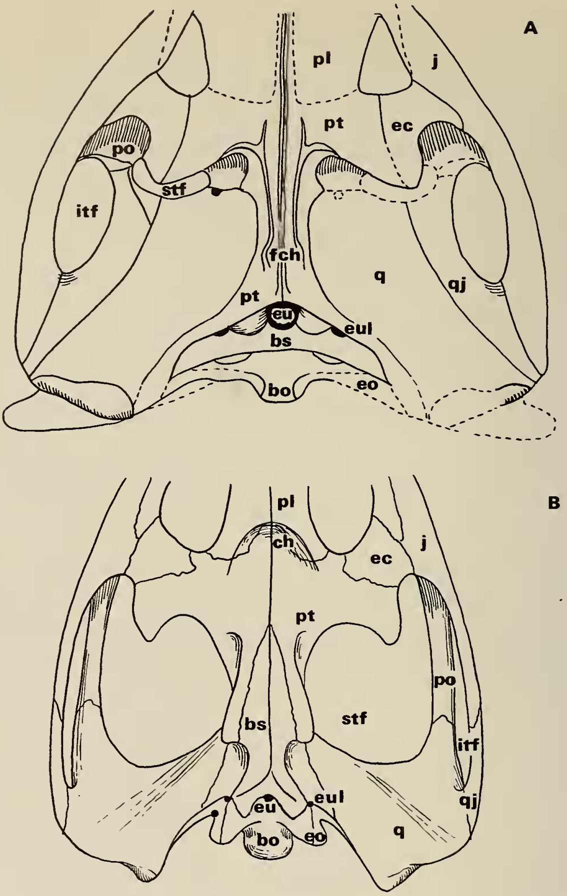

Fig. 33. Basicranial region of the skulls of A. *Orthosuchus stormbergi* (natural size). B. *Steneosaurus durobrivensis*, after Andrews (1913*a*) ($\frac{1}{6}$ natural size).

In *Orthosuchus*, as in *Steneosaurus* and *Pelagosaurus*, the flange of the pterygoid does not project below the level of the alveolar border to the same extent as seen in recent crocodiles. This downward movement of the flange in living crocodiles has involved a change in orientation of the ectopterygoid, so that it lies essentially in a vertical position. In *Orthosuchus* and *Steneosaurus* it is more or less horizontal.

Mesosuchians, again, differ from *Orthosuchus* in that the palatine forms part of the wall and floor of the secondary palate. This is brought about by fusion of the palatines ventrally in the midline, and has also resulted in the enlargement of the postpalatine fenestra on each side. In forms like *Pelagosaurus* and *Pholidosaurus* (Andrews 1913*b*) the choanae are large and confluent, and the anterior border is formed by the palatine and the pterygoid forms the roof.

In recent crocodiles the pterygoids also contribute to the secondary palate and are hollowed out behind the palatines and between the pterygoid flanges so that the narial tubes are continued posteriorly. The ridges on the body of the pterygoids of *Orthosuchus* mark the position of the choanae in eusuchians (Fig. 34). A transitional stage between these is seen in the mesosuchian *Theriosuchus* (Joffe 1967) where the internal nares lie in a depression which is walled laterally by the pterygoids and roofed by the palatines.

The prefrontal of *Orthosuchus* forms an internal process which extends down towards the palate. In living crocodiles this process unites with that from the other side in the midline, and also with the palatine and pterygoid. A similar process occurs in *Pelagosaurus* British Museum (Natural History) No. 32599 and also in *Steneosaurus* and *Metriorhynchus*, though it is incomplete in each case. Andrews (1913*a*) was of the opinion that in the latter types these processes did meet in the midline and also met the palatine ventrally.

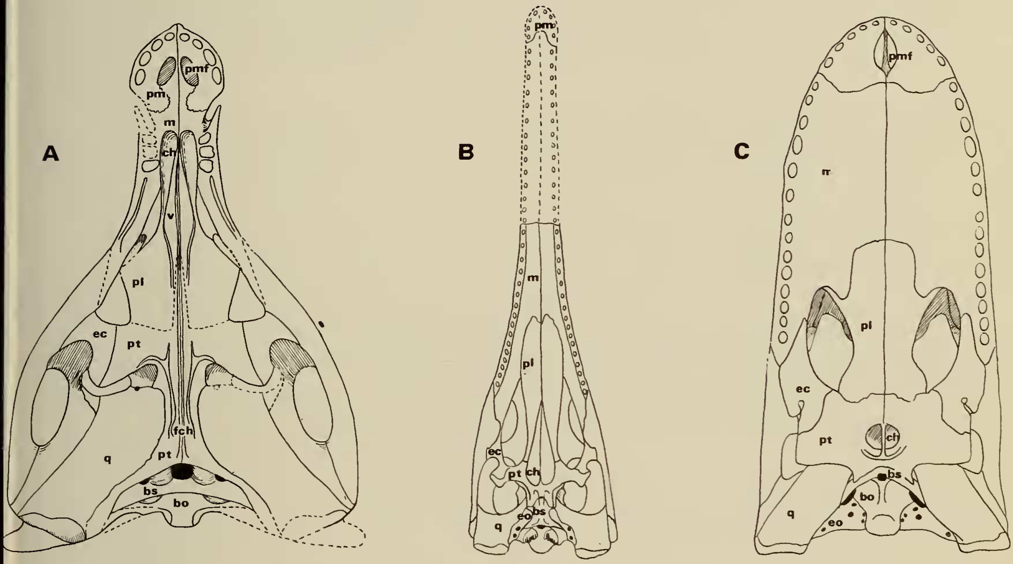

Fig. 34. The palate of the skulls of A. *Orthosuchus stormbergi* ($\frac{2}{3}$ natural size). B. *Pelagosaurus typus*, after Eudes-Deslongchamps (1864) ($\frac{2}{9}$ natural size). C. *Alligator mississippiensis*, after Kalin (1955) ($\frac{2}{5}$ natural size).

The symphysial region of the lower jaw of *Protosuchus* is unknown, but in *Notochampsa* (Haughton 1924) and *Orthosuchus* it is short. In *Protosuchus* and many thecodontians the rear end of the lower jaw lacks the marked prolongation of the angular and articular bones that characterizes mesosuchians and eusuchians, and this is probably also the case in *Orthosuchus*.

Orthosuchus is the first Triassic crocodile known to possess a prearticular (the internal surface of the lower jaw is unknown in *Protosuchus*) and, indeed, this element is known in only two other crocodilians. It is well developed in *Pelagosaurus*, of Lower Jurassic age, but in the Upper Jurassic form *Metriorhynchus* it is quite short. It is absent as a separate element in Crocodilia from more recent strata. In contemporary crocodilians, where the prearticular fuses with the articular during development (De Beer 1937) the region normally occupied by the prearticular is filled by a medial process of the angular. The gradual elimination of the prearticular through the Crocodilia is shown in Figure 35.

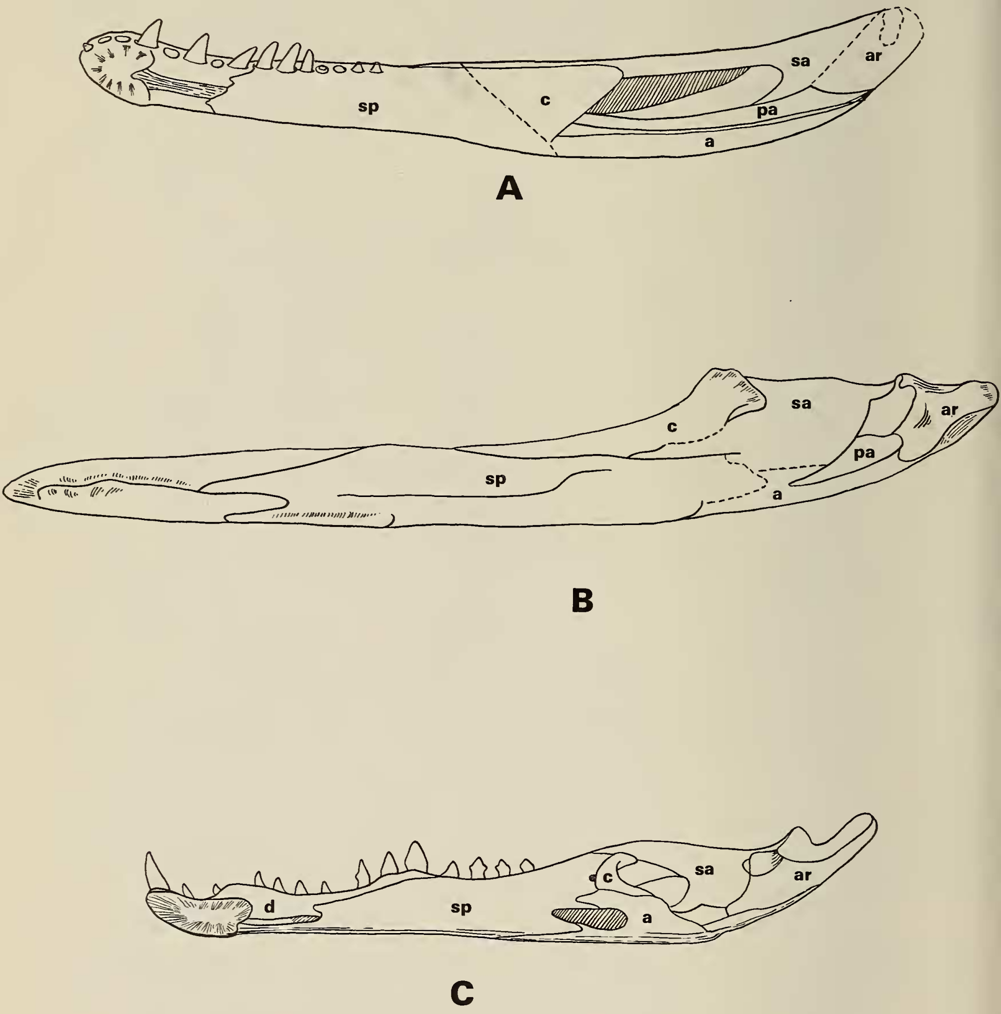

Fig. 35. Medial view of the lower jaws of A. *Orthosuchus stormbergi* (natural size). B. *Metriorhynchus cultridens*, after Andrews (1913*a*) ($\frac{1}{6}$ natural size). C. *Crocodylus vulgaris*, after Kalin (1955) ($\frac{1}{3}$ natural size).

Although the entire vertebral column of *Protosuchus* is known, it is obscured dorsally, and to a lesser extent ventrally, by scutes. Colbert & Mook (1951) estimated a presacral count of 24 vertebrae, as is suggested for *Orthosuchus*. All early crocodilians possess thecodontian spool-shaped, amphicoelous vertebrae, and this condition was retained generally among mesosuchians. The anterior vertebrae are keeled in *Orthosuchus*, but in the marine Jurassic crocodiles this keeling is lost. In living crocodiles keeling has been extended to include the anterior dorsals.

A similar change in position of the rib facets through the cervical series back down the column occurs in both *Protosuchus* and *Orthosuchus*. In *Protosuchus* the parapophysis lies at the base of the transverse process above the neurocentral suture on vertebra twelve, and in this respect shows an identical condition to that seen in *Orthosuchus*. Further, in both types the two rib facets remain distinct up to the last presacral vertebra, a condition retained in forms like *Steneosaurus*.

Protosuchus and *Orthosuchus* also share the primitive count of two sacral vertebrae. In both forms, and in later crocodiles, the extremities of the sacrum are large because each sacral rib articulates both with the centrum and with the transverse process.

The cervical ribs of *Protosuchus* and *Erythrochampsa* (Broili & Schröder 1936) closely resemble those of *Orthosuchus*, but are also indistinguishable from those of many thecodontians as seen in *Ticinosuchus*.

The dorsal ribs of *Protosuchus* are of particular interest, and are identical to those of *Orthosuchus*. In both types the shaft is flanked by an antero-ventral and a postero-dorsal flange. In the thecodontians *Euparkeria* and *Ticinosuchus*, they are not flanged in this way, while in teleosaurs only anterior flanges are developed in the first two or three dorsal ribs.

The scapulae of *Orthosuchus*, *Protosuchus* and *Notochampsa* are strikingly similar in shape. They are crocodilian in form in that the upper end is expanded, particularly posteriorly, and is very much larger in size than the lower end. This expansion is not found in teleosaurs (Fig. 36), but this no doubt is an aquatic adaptation. However, the coracoids of these forms are closely similar in shape, and are elongate elements expanded both proximally and distally. This represents an advanced stage over that seen in typical thecodontians where the coracoid is rather an insignificant element, subcircular in shape.

In addition, these early crocodilians differ from, and are more specialized than, thecodontians in that they lack a clavicle. Von Huene (1925) did suggest that a clavicle is present in *Notochampsa*, though Broom (1927) expressed the opposite view and believed the element in question to be a scute. Broom appears to have been correct in this.

In 1924 Haughton expressed doubts concerning the crocodilian form of the humerus of *Notochampsa*. He was of the opinion that it is more thecodontian in form, much like that of *Stagonolepis*. However, the description does not support this view, and the recent find of *Notochampsa* includes two humeri which are

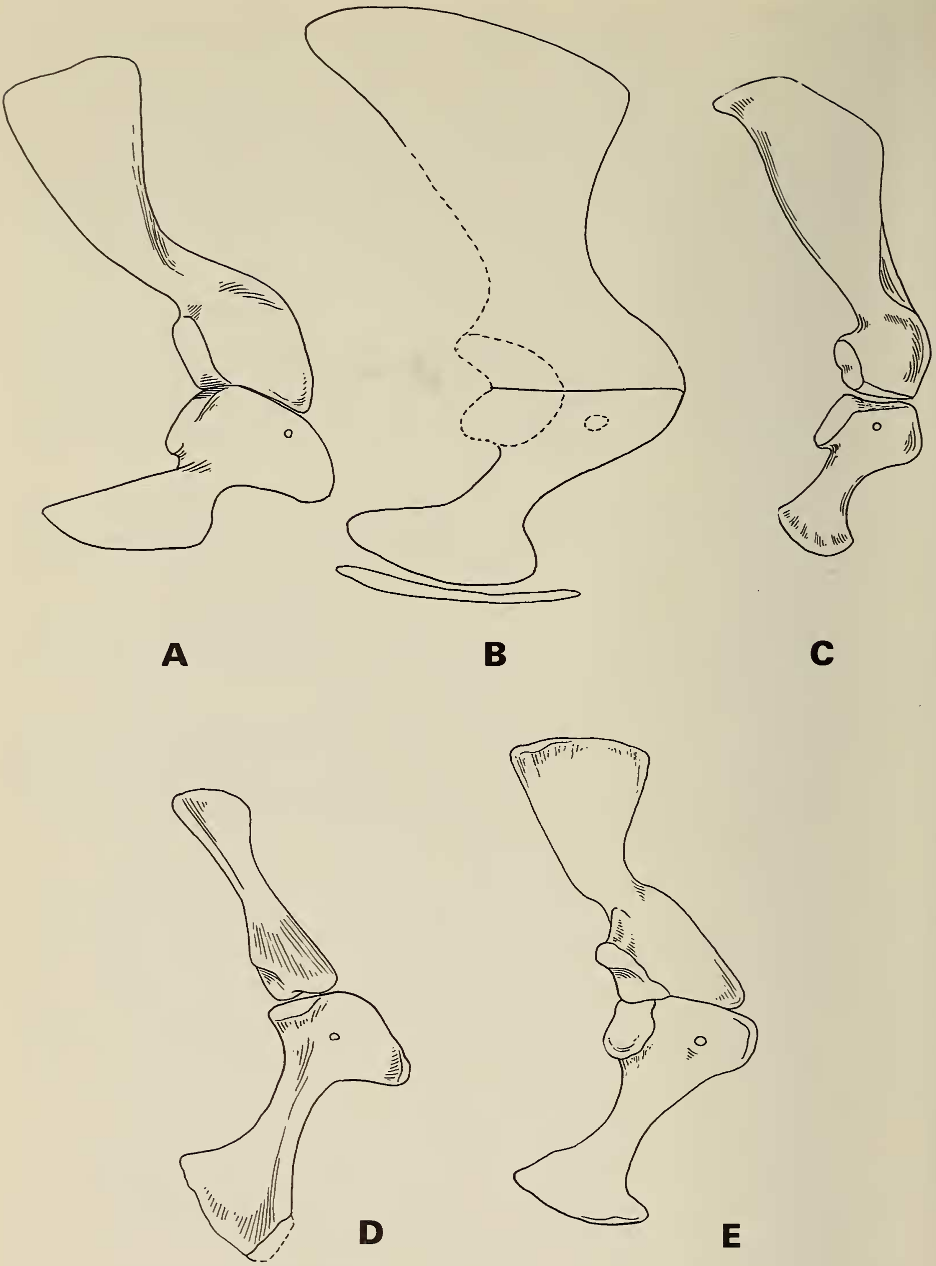

Fig. 36. Lateral views of the pectoral girdles of A. *Prctosuchus richardsoni*, after Colbert & Mook (1951) (natural size). B. *Notochampsa istedana*, after Broom (1927) (natural size). C. *Orthosuchus stormbergi* (natural size). D. *Steneosaurus durobrivensis*, after Andrews (1913*a*) (⅓ natural size). E. *Crocodylus acutus* (= *C. americanus*) (reversed), after Mook (1921*b*) (⅕ natural size).

very similar to those of *Orthosuchus* and *Protosuchus*. In these forms, as in living crocodiles, the humerus bears a deltopectoral crest which rises to an apex about one-third of the way down a long slender shaft.

A very striking crocodilian character can be seen in the form of the carpus. Broom (1927) commented on the metacarpal-like nature of the radiale and ulnare in *Notochampsa*, and an identical condition is present in both *Protosuchus* and *Orthosuchus*. In the latter form the ulnare is only just shorter than the longest metacarpal (the third), and the radiale is more than one and a half times its length. Hence, as in modern crocodiles, the carpus is elongated to add an extra segment to the fore-limb.

Protosuchus further resembles *Orthosuchus* in that a large pisiform element is preserved in the carpus. However, in *Orthosuchus* two distal carpals are present, whereas in *Protosuchus* and *Notochampsa* there is only one (Fig. 37). In these forms the distal carpal lies in articulation with the ulnare.

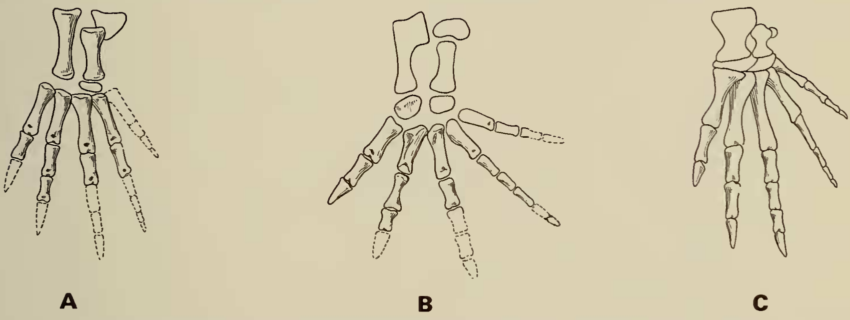

Fig. 37. Carpus and manus of A. *Protosuchus richardsoni* (reversed), after Colbert & Mook (1951) (⅔ natural size). B. *Orthosuchus stormbergi* (⅔ natural size). C. *Crocodylus*, after Romer (1956).

The pelvis in *Orthosuchus* is closely similar to that of *Protosuchus*. In both the acetabulum is perforated ventrally, a feature separating these forms quite clearly from all thecodontians where the acetabulum is imperforate. The ischia are also very alike and resemble that of *Erythrochampsa*. The most significant feature here is the development of the anterior process to exclude the pubis from the acetabulum. Unfortunately, on neither side of the body is the pubis of *Erythrochampsa* complete, although Broom was of the opinion that the pubis does not enter the acetabulum.

In all three forms the iliac blade is produced anteriorly to form a bluntly-pointed process. This was reduced in teleosaurs, and only a vestige remains in eusuchians (Fig. 38). In *Orthosuchus*, anterior to the acetabulum, the ilium is notched. The inner of the two processes meets the ischium, and the outer, together with the ischium, articulates with the pubis. A similar condition probably exists in *Protosuchus*. In *Steneosaurus* the head of the pubis occupies a more ventral position, and in living crocodiles the pubis articulates only with the ischium.

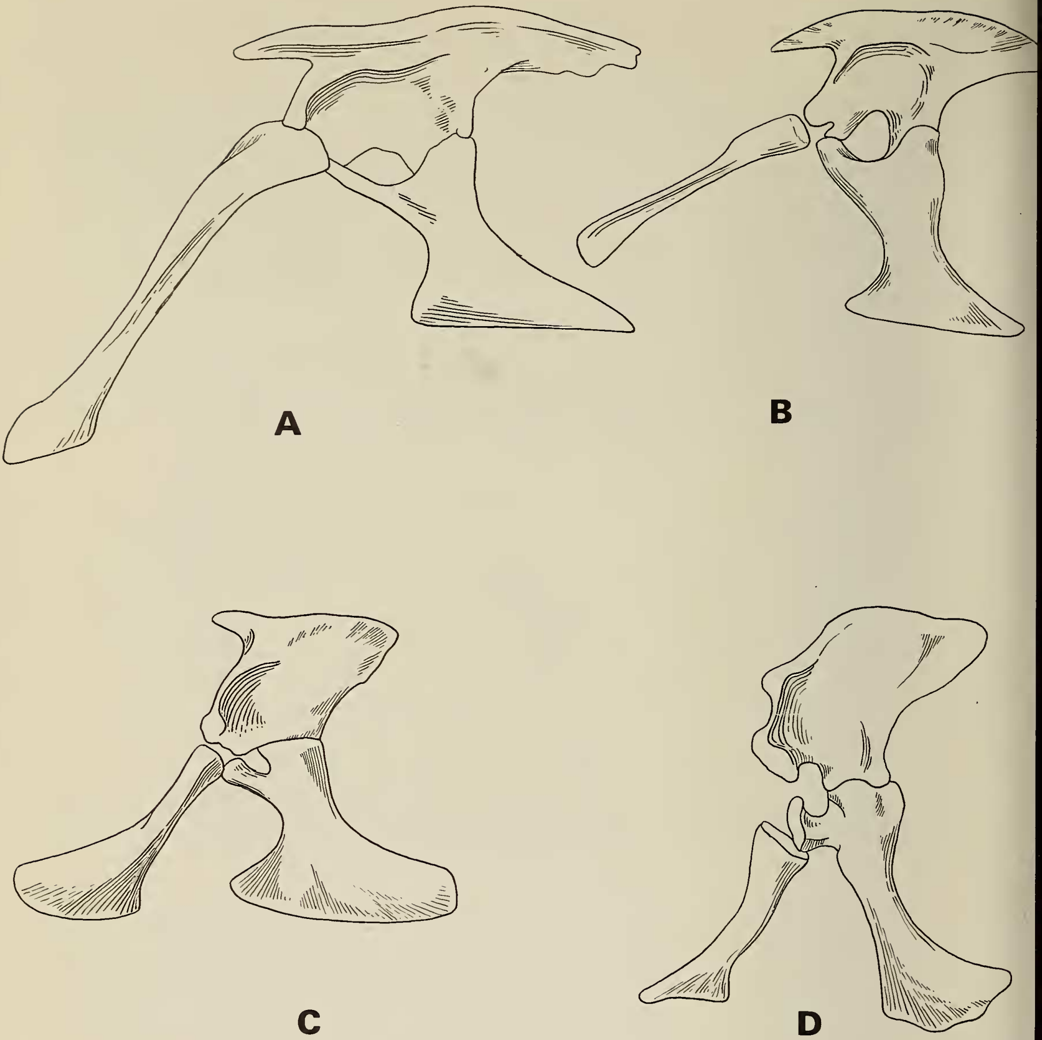

Fig. 38. Lateral views of the pelvic girdles of A. *Protosuchus richardsoni* (reversed), after Colbert & Mook (1951) (natural size). B. *Orthosuchus stormbergi* (natural size). C. *Steneosaurus leedsi*, after Andrews (1913*a*) ($\frac{1}{4}$ natural size). D. *Alligator*, after Romer (1956).

The femur of *Orthosuchus* is remarkably similar to that of *Protosuchus*, and in fact differs little from that of living crocodiles. The tibia lacks a distinct cnemial crest in each case. Similarly, there is little difference between the tarsus of *Orthosuchus* and that of *Protosuchus*. In both types the calcaneum bears a tuber which is more prominently developed than it is in living crocodiles and which is grooved on its posterior surface. However, whereas in *Orthosuchus* there are two distal tarsals, in *Protosuchus* only one is known.

The structure of the tarsus of *Erythrochampsa* is difficult to determine. According to Haughton (1924) it consists of two proximal and two distal elements. The calcaneum bears a small posterior tuber. Broom (1927) described the same tarsus as similar to that of the Upper Jurassic mesosuchian *Alligatorellus*. Lortet (1892) had incorrectly described three distal tarsals in this type, but Broom figured the tarsus of *Erythrochampsa* as consisting of astragalus and calcaneum only. At most, only two elements can be identified in the type, as shown by Broom, though it is questionable as to what these are.

The metatarsus of *Orthosuchus* is composed of four elongated metatarsals with the fifth reduced to a hook and held behind the other four. *Protosuchus* shows a similar condition. Broom (1904) described four digits in *Erythrochampsa*, but in 1927 figured four elongated elements and a short, hook-shaped fifth. Von Huene (1925) figured the same specimen showing four elongated and a slightly shortened fifth metatarsal in articulation with two phalanges.

At my request, Dr M. A. Cluver (South African Museum) examined the type specimen and came to the conclusion that both Broom and Von Huene had misinterpreted the specimen. Broom gave the correct number of unreduced metatarsals (four), but did not indicate that the fourth is incomplete. Von Huene miscounted and regarded the broken fourth metatarsal as a fifth member and figured it in articulation with phalanges. Although the material is difficult to interpret, there is a piece of bone underlying the proximal end of the fourth metatarsal which does not seem to be part of the distal end of the tibia or fibula. This could well be a reduced fifth metatarsal. On balance it seems likely that the metatarsus of *Erythrochampsa* is identical to that of both *Orthosuchus* and *Protosuchus* (Fig. 39). In view of this, it is unfortunate that Kalin (1955) chose to reproduce Von Huene's incorrect figure.

Protosuchian armour may be distinguished from thecodontian armour by a combination of characters. The dorsal scutes are arranged in two rows, with the anterior margin of each overlapped by the preceding scute. The articular surface of each dorsal scute is smooth, and behind this the exposed surface is strongly pitted. Further, the lateral portion of each scute is strongly bent downward and the bend is strengthened by a dorsal ridge.

Many mesosuchians such as *Alligatorellus* show an identical development of dorsal armour. In others like *Crocodileimus* (Lortet 1892), although the scutes covering the neck and lumbar region are paired, the mid-dorsals are arranged in four rows. In living genera as many as ten scutes may be present in a row.

The most anterior scutes of the dorsal armour of *Orthosuchus* and *Notochampsa* carry a peg-like process which extends forward from the anterior margin of the dorsal ridge, and fits into a groove on the ventral surface of the preceding scute. This feature is inherited from thecodontians, and is one which was passed on to at least some of the mesosuchians, like *Steneosaurus*, *Pholidosaurus* and *Goniopholis*.

Although ventral armour of the type specimen of *Notochampsa* is not known, five ventral scutes form part of the material of specimen British Museum

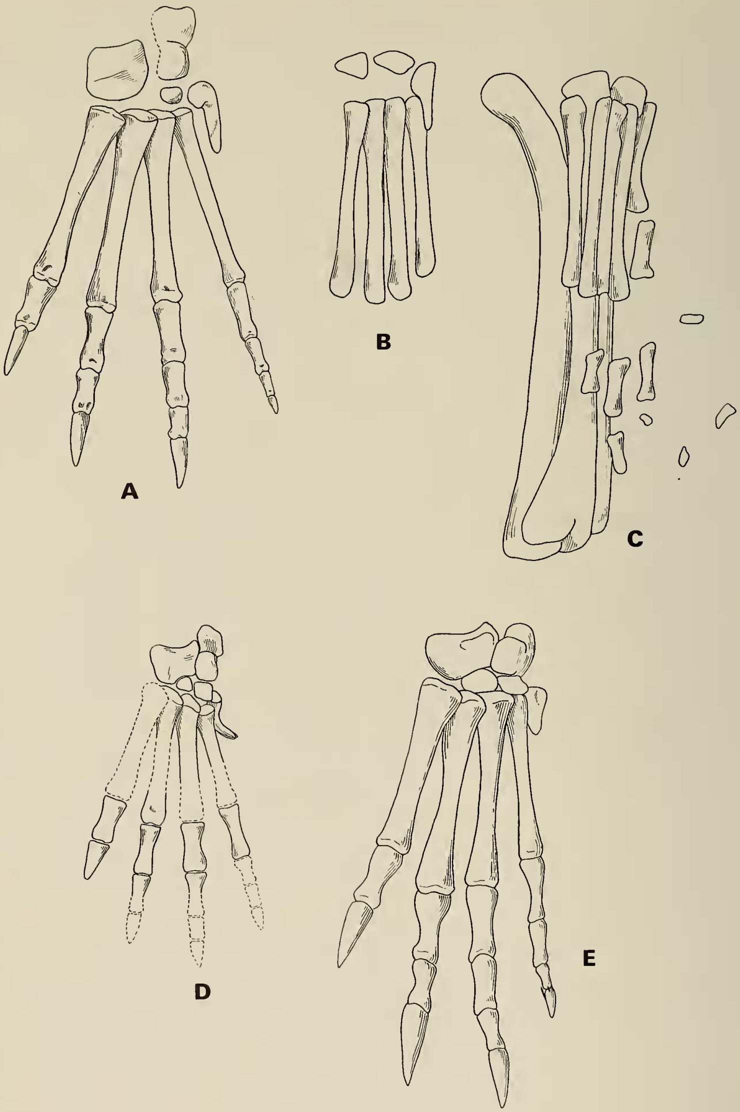

Fig. 39. Tarsus and pes of A. *Protosuchus richardsoni* (reversed), after Colbert & Mook (1951) (⅔ natural size). B. *Erythrochampsa longipes*, after Broom (1927). C. *Erythrochampsa longipes* (reversed), after Von Huene (1925). D. *Orthosuchus stormbergi* (⅔ natural size). E. *Crocodylus*, after Romer (1956).

(Natural History) No. R8503. *Protosuchus* and *Erythrochampsa* were also protected by dorsal and ventral, but not lateral scutes, except over the tail. Probably *Orthosuchus*, too, was covered in this way, though its ventral armour is as yet unknown. The teleosaur *Mystriosaurus* has a similar covering of ventral armour, and it is also found in *Crocodileimus* and *Pholidosaurus*, although here the scutes are polygonal in shape. Ventral armour is not known in atoposaurs, and is generally absent in living crocodiles.

Ventrally and at the level of the distal portion of the pubis, both *Orthosuchus* and *Protosuchus* show an accumulation of gastralia. In life these were probably more numerous and extended farther forwards. Gastralia are known in some mesosuchians, like *Atoposaurus* and *Alligatorellus*, and are present in eusuchians.

LIMB AND LIMB GIRDLE PROPORTIONS IN CROCODILIA AND THECODONTIA

Relationship between lengths of scapula and humerus (Fig. 40)

The relationship between length of scapula and length of humerus for the seven available pairs of measurements on contemporary animals may conveniently be shown by plotting $\log_{10}$ humerus length (x axis) against $\log_{10}$ of scapula (y axis). They may be represented by the regression line $y = 1{,}167x - 0{,}522$. If Y and X are the actual lengths of scapula and humerus respectively, the equation becomes $Y = 0{,}301X^{1{,}17}$.

The regression coefficient 1,167 is significantly different from 1,0 ($t = 4{,}674$ with 5 d.f.). This shows that the scapulae of these contemporary crocodilians increases in length at a proportionally greater rate than the humerus, i.e. the ratio between the two is greater in the larger animals.

In Figure 40 are included points for selected fossil crocodilians and thecodontians, though of these the thecodontians *Vjushkovia* and *Euparkeria*, and the protosuchians *Orthosuchus* and *Protosuchus*, form a group of very ancient animals which may reasonably be separated from the mesosuchians, whether land or marine forms.

The regression coefficient for the above four is given by $b = 1{,}170$. This is patently not significantly different from the above value 1,167. The separation of these two regression lines is however significant at the 1% level ($t = 3{,}780$ with 7 d.f.). That is, these four animals form a group separate from the contemporary crocodilians. The equation for the above four is: $y_1 = 1{,}170x_1 - 0{,}3107$ so that the initial dimensions are related by: $Y_1 = 0{,}489X_1^{1{,}17}$.

Comparing this with the previous equation it is seen that in these forms the ratio of scapula length to humerus length is about 1,6 times as great, for any particular value of scapula length. These higher ratios are in fact very apparent in Table 4, and clearly apply to *Orthosuchus*. The very high value of the ratio for *Vjushkovia* is not out of place, and can be attributed to the fact that it is a member of this ancient group, and is a very large animal.

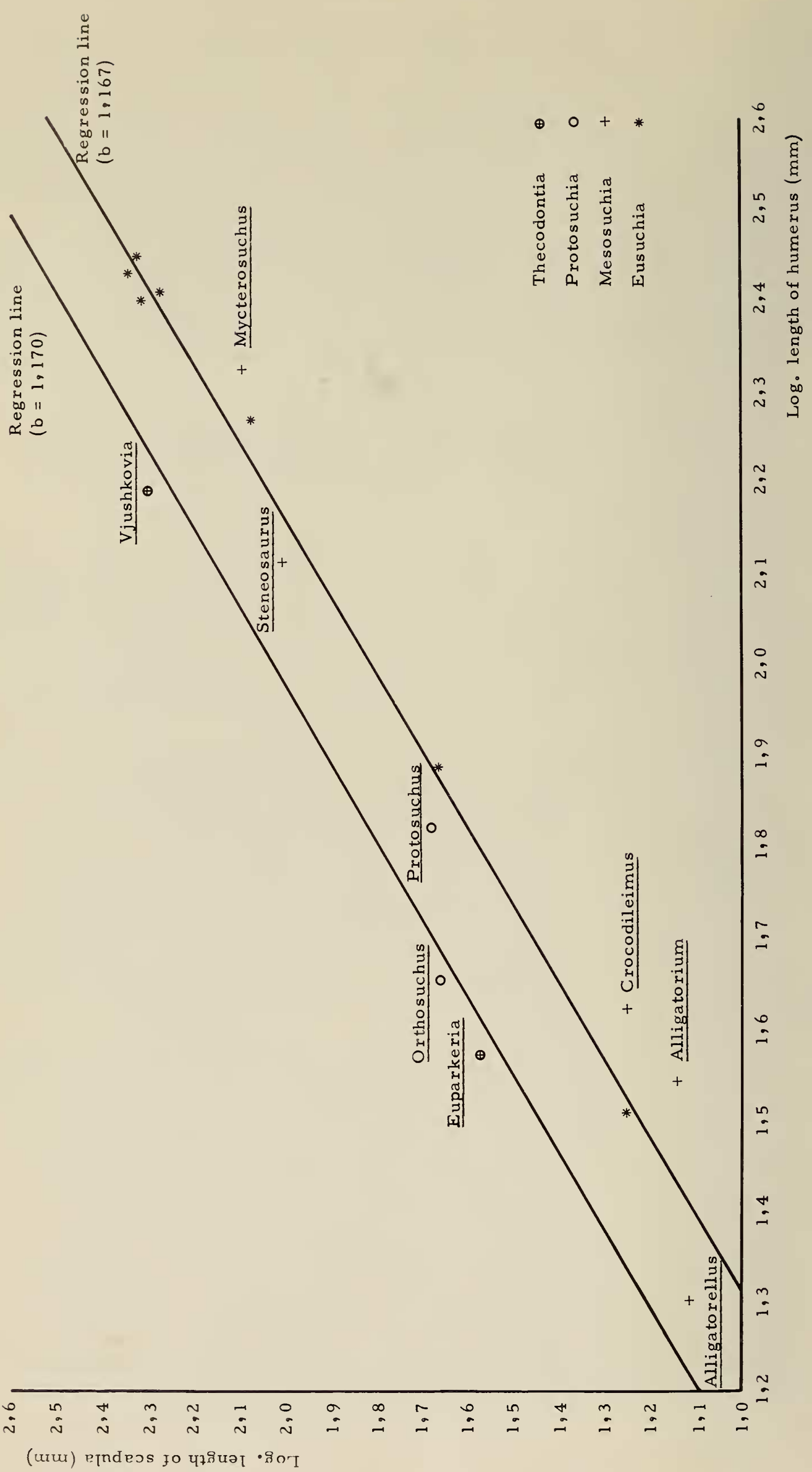

Fig. 40. Graph showing the relationship between lengths of scapula and humerus (shown in log. form) for selected living and fossil crocodilians and thecodontians.

Table 4

Comparison of proportions in selected thecodontians and crocodilians

	Thecodontia			Protosuchia		Mesosuchia						Eusuchia							
	Chasmatosaurus yuani Data from Young (1936)	*Vjushkovia triplicostata* Von Huene (1960)	*Euparkeria capensis* SAM-5867 Ewer (1965)	*Orthosuchus stormbergi* SAM-K409	*Protosuchus richardsoni* A.M.N.H. No. 3024 Colbert & Mook (1951)	*Steneosaurus leedsi* B.M.N.H. No. R3806 Andrews (1913*a*)	*Mycterosuchus nasutus* B.M.N.H. No. R2617 Andrews (1913*a*)	*Alligatorellus beaumonti* Lortet (1892)	*Alligatorium meyeri* Lortet (1892)	*Crocodileimus robustus* Lortet (1892)	*Theriosuchus pusillus* B.M.N.H. No. 48216	*Alligator mississippiensis* (juvenile)	*Alligator mississippiensis* Zool. Mus. ZH. Ex. 13180 Krebs (1963*a*)	*Crocodylus porosus* (juv.) A.M.N.H. No. 69125 Colbert & Mook (1951)	*Crocodylus porosus* B.M.N.H. No. 1902. 12.19.1	*Crocodylus niloticus* B.M.N.H. No. 1969. 1565	*Crocodylus niloticus* B.M.N.H. No. 111.11.1.1.89a	*Crocodylus acutus* B.M.N.H. gallery specimen	*Crocodylus acutus* A.M.N.H. No. 7139 Mook (1921*b*)
Scapula/humerus (%)	—	121,2	98,9	102,2	72,7	78,5	63,9	65,0	40,0	42,9	—	55,9	—	59,7	75,0	74,5	82,0	64,9	82,1
Coracoid/scapula	—	59,0	—	50,0	52,1	98,0	111,1	46,2	100,0	88,9	—	100,0	—	91,3	90,5	100,0	92,7	100,0	90,5
Radius/humerus	—	81,8	84,1	87,8	78,8	51,5	54,5	82,5	80,0	66,7	78,9	69,9	65,0	59,7	57,1	52,9	57,2	59,5	55,6
Radiale/radius	23,7	—	—	41,3	26,9	—	—	30,3	33,9	37,5	—	24,4	—	21,7	—	27,4	28,0	29,1	—
Tibia/femur	—	88,0	85,7	93,9	83,0	50,7	50,0	95,8	85,1	70,9	88,9	82,2	77,3	74,4	68,1	60,9	65,7	71,8	69,8
Humerus/femur	—	66,0	67,7	78,9	66,0	43,0	52,8	83,3	73,7	76,4	70,4	88,2	89,6	89,5	87,5	79,7	84,2	94,9	82,5
Humerus + radius + radiale/ femur + tibia . . .	—	—	—	91,2	72,1	—	—	88,3	82,9	85,6	—	90,5	—	86,7	—	82,9	88,0	97,6	—
Femur + tibia/length of trunk	—	—	—	65,0	—	—	—	—	—	—	—	61,0	—	—	50,0	52,0	44,0	49,0	—

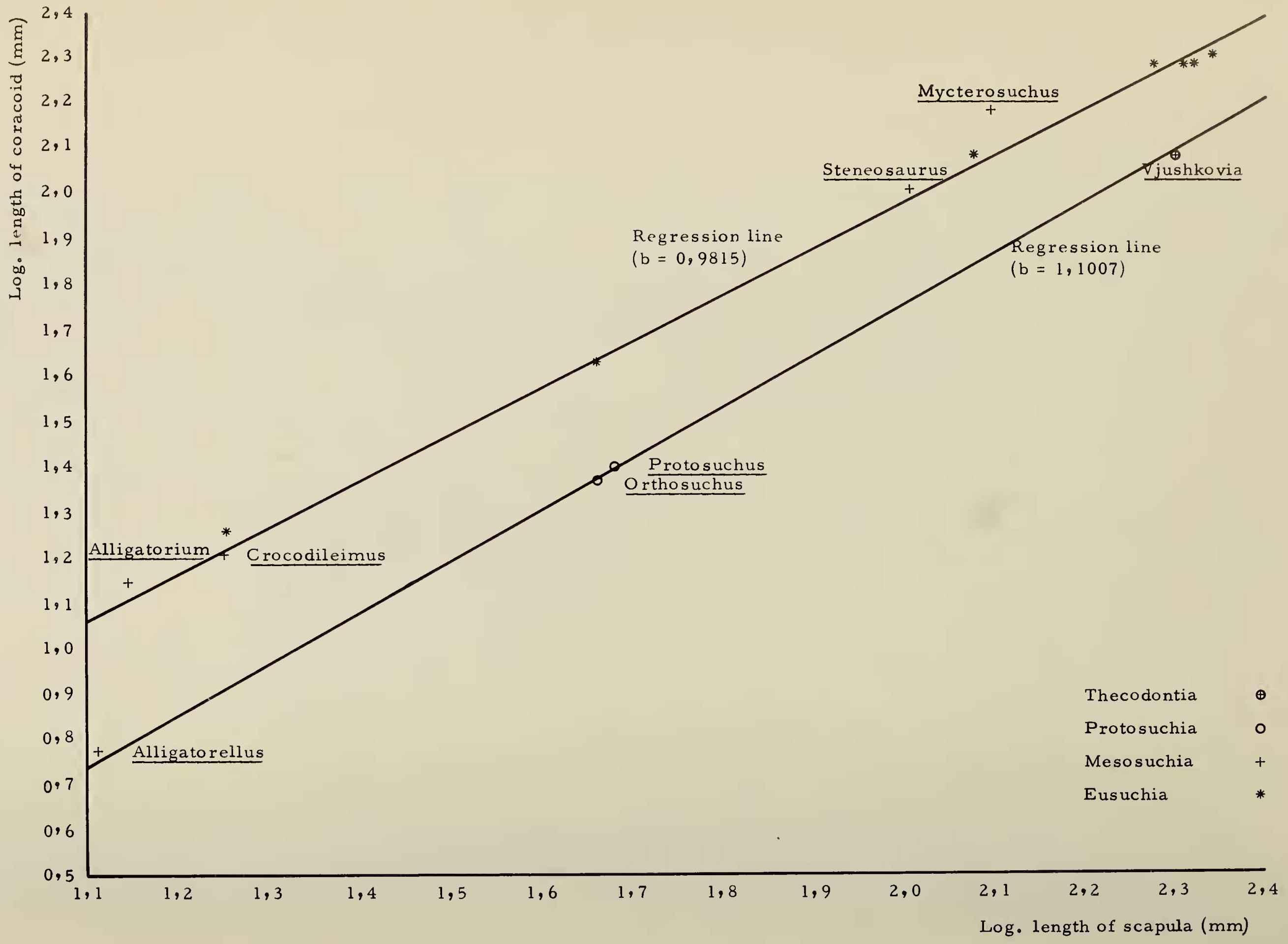

Fig. 41. Graph showing the relationship between length of coracoid and scapula (shown in log. form) for selected living and fossil crocodilians and thecodontians.

The mesosuchians on this graph show rather more scatter than the eusuchians, but no different trends. The regression slope, and the relationship with size which it shows, appear to be applicable to all of these forms.

Relationship between lengths of scapula and coracoid (Fig. 41)

It can be seen from Table 4 that in the thecodontian *Vjushkovia*, and the protosuchians *Orthosuchus* and *Protosuchus*, the coracoid is approximately half as long as the scapula, whereas in the modern crocodilians these elements are more or less equal in length. The relationships may be shown when $\log_{10}$ scapula is plotted against $\log_{10}$ coracoid. This has been done for all contemporary and fossil forms.

Two regression lines are of interest. The regression of log coracoid (y) on log scapula (x) for the seven contemporary forms is given by: $y = 0{,}9815x + 0{,}0150$. The regression for *Vjushkovia*, *Orthosuchus* and *Protosuchus* however is given by: $y_1 = 1{,}1007x_1 - 0{,}4605$.

The difference between the coefficients 0,9815 and 1,1007 in the above equations is significant at the 5% level.

It now becomes interesting to note that *Steneosaurus*, *Alligatorium* and *Crocodileimus* lie closely on the first line, while *Alligatorellus* lies virtually on the second. *Mycterosuchus* is remarkable in that the scapula is actually shorter than the coracoid, but this is surely due to aquatic adaptation.

It is also surprising to find that *Vjushkovia* falls into a group with the protosuchians, since in thecodontians the coracoid is normally less elongate relative to the scapula than it is in crocodilians. In forms like *Euparkeria* and *Stagonolepis*, for example, the coracoid is considerably wider than it is high.

Relationship between lengths of humerus and radius (Fig. 42)

The relationship between lengths of radius (Y) and of humerus (X) in fossil and contemporary forms is again best seen in a plot of $y = \log Y$ against $x = \log X$. All available values have been plotted.

Two regression lines are given, one for the thecodontians *Vjushkovia* and *Euparkeria*, together with the protosuchians *Orthosuchus* and *Protosuchus* (upper line, $b = 1{,}007$), and the other for the eight contemporary crocodilians (lower line, $b = 0{,}9028$).

The lower line has a regression coefficient significantly smaller than 1,0 ($t = 3{,}721$, significant at the 1% level). The regression coefficients of the two lines, however, are not significantly different ($t = 1{,}811$). The spatial separation of the two lines though is significant at the 1% level. Thus the difference between these two groups of animals is well established on this evidence.

The radius/humerus ratios in *Orthosuchus* and *Protosuchus* and in the thecodontians *Vjushkovia* and *Euparkeria* are all very similar and very much higher than in the living genera. This high ratio was retained, or very nearly, by certain of the small mesosuchians *Alligatorellus*, *Alligatorium* and *Theriosuchus*. However, in *Crocodileimus*, a mesosuchian of similar age and size, the radius is

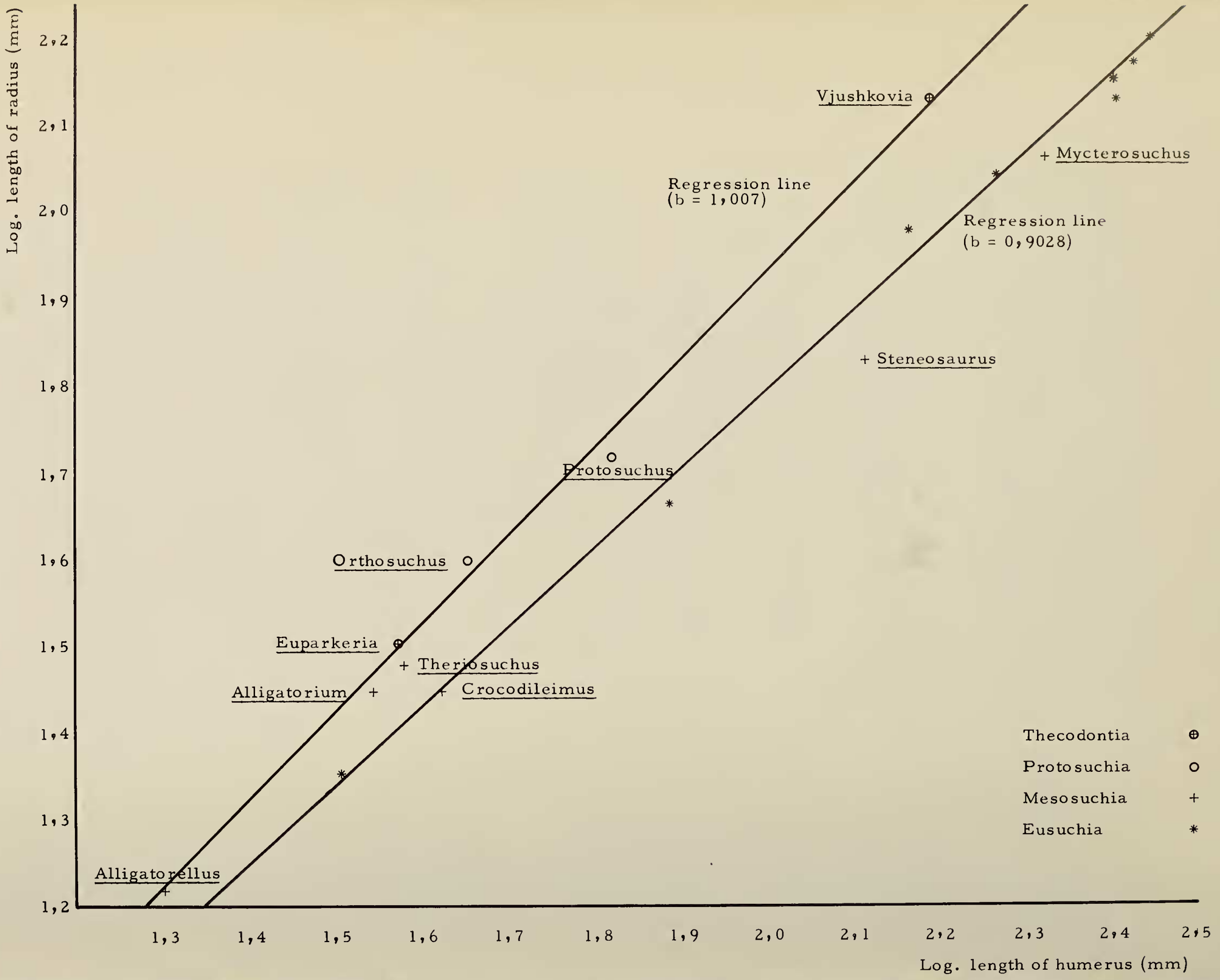

Fig. 42. Graph showing the relationship between lengths of radius and humerus (shown in log. form) for selected living and fossil crocodilians and thecodontians.

shorter relative to the length of the humerus. This animal agrees well, in respect of radius/humerus ratio, with living genera. In these the ratio, in each case, is less than 0,70, the ratio becoming smaller in older (i.e. larger) animals. In the more fully aquatic mesosuchians like *Steneosaurus*, the ratio is rather similar to that in contemporary crocodiles.

Relationship between lengths of radius and radiale

Data is available here for the thecodontian *Chasmatosaurus*, the protosuchians *Orthosuchus* and *Protosuchus*, the mesosuchians *Alligatorellus*, *Alligatorium* and *Crocodileimus*, and for five contemporary crocodiles. In each of these the radiale is an elongate bone, averaging in the eleven examples about 29,5 % of the length of the radius. In *Orthosuchus* it is 41,3 % of the length of the radius. This is significantly longer, relative to the radius, than in the other ten animals above (significant at the 5 % level).

Relationship between lengths of femur and tibia (Fig. 43)

This relationship is again brought out in a plot of $\log_{10}$ tibial length against $\log_{10}$ length of femur. On this evidence there is no reason for separating the mesosuchians from the contemporary crocodiles, though the thecodontians and protosuchians could at first sight be supposed somewhat different, as could the more fully aquatic forms.

The regression coefficient for the mesosuchians and modern forms taken together is $b = 0{,}8822$. The difference between this value and 1,0 is significant at the 0,1 % level. The relationship between length of femur (X) and length of tibia (Y) for these specimens is represented by: $Y = 1{,}31X^{0{,}88}$.

This equation shows that the relative length of tibia to length of femur decreases significantly as the size of the animal increases. In other words, the tibia elongates more slowly than the femur.

The thecodontians *Vjushkovia* and *Euparkeria*, and the protosuchians *Orthosuchus* and *Protosuchus*, lie rather above this line, and *Steneosaurus* and *Mycterosuchus* below it.

The regression coefficient for the thecodontians and protosuchians is $b = 1{,}0125$ and is not significantly different from $b = 0{,}8822$ above ($t = 2{,}038$ with 12 d.f.). A test for the separation of the two lines, however, gives $t = 3{,}768$ with 12 d.f., significant at the 1 % level, hence showing the thecodontians and protosuchians to have significantly higher tibia/femur ratios at corresponding animal sizes than the mesosuchians and eusuchians.

The tibia is therefore long relative to the length of the femur in *Orthosuchus* and *Protosuchus*, as in the thecodontians *Euparkeria* and *Vjushkovia*. In eusuchians, the femur grows at a faster rate than the tibia during development from juvenile to mature stage, so that the tibia/femur ratio decreases with age (i.e. size). The more fully aquatic *Steneosaurus* and *Mycterosuchus* have very low tibia/femur ratios, *ca* 0,50, values which are low even though the large sizes of these forms are taken into account. In *Metriorhynchus* this value is further reduced to about 0,40, and this again is clearly a result of aquatic adaptation.

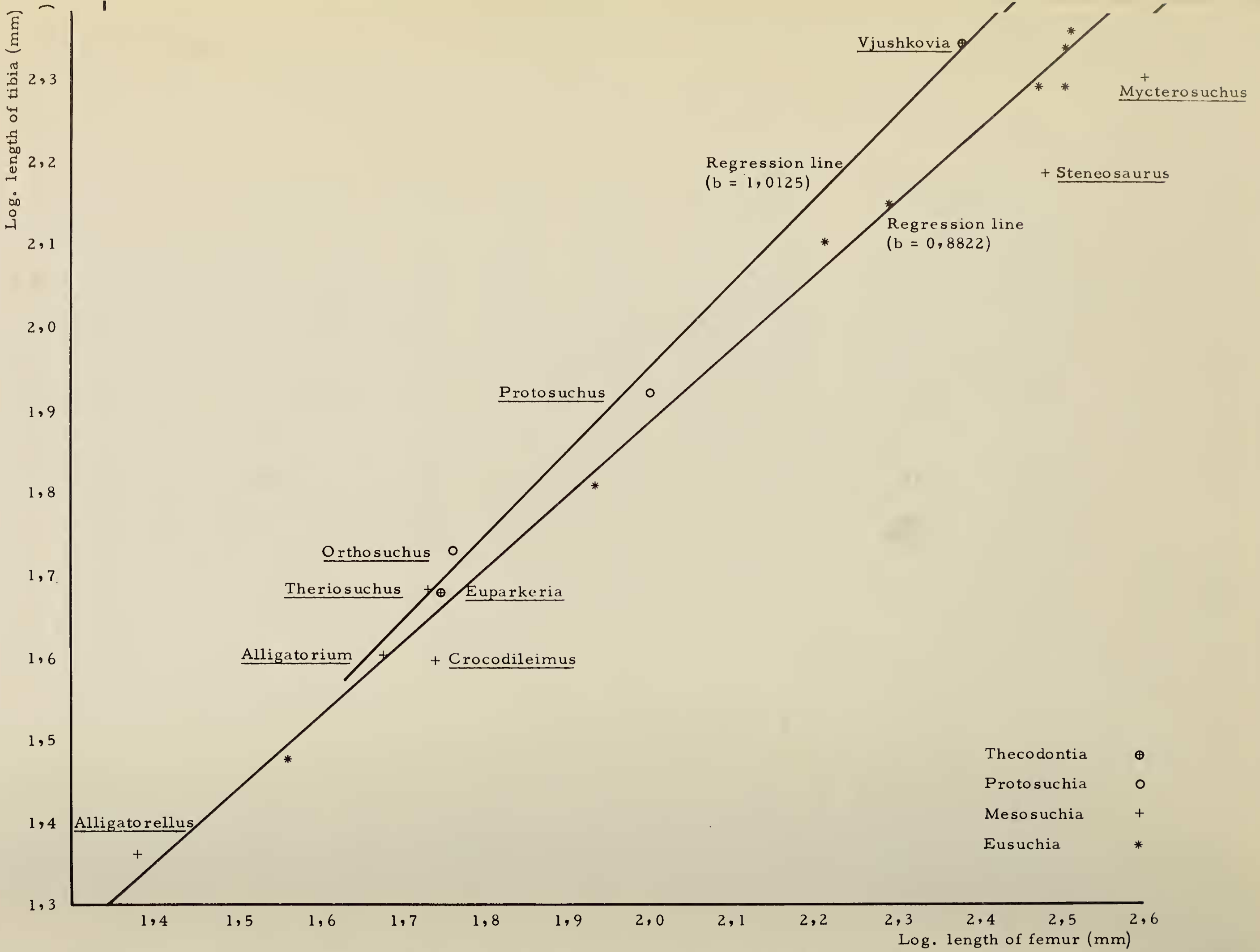

Fig. 43. Graph showing relationship between lengths of tibia and femur (shown in log. form) for selected living and fossil crocodilians, and thecodontians.

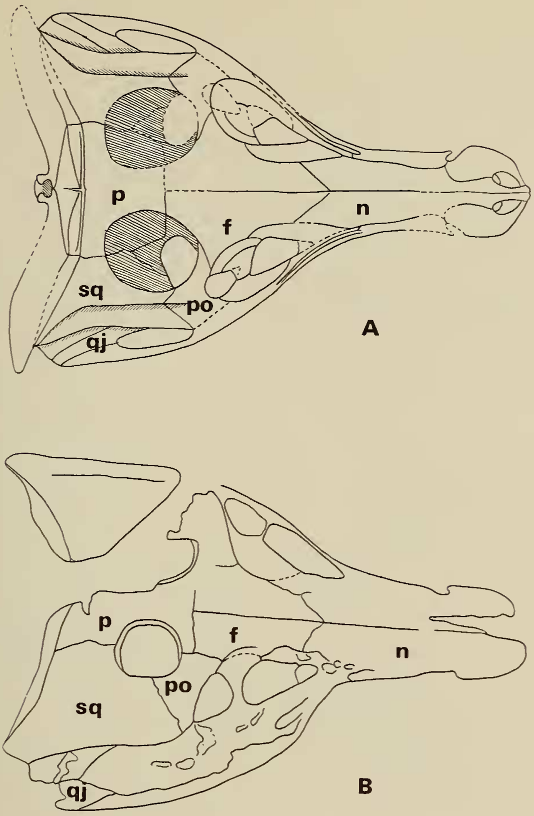

Fig. 44. Dorsal views of the skulls of A. *Orthosuchus stormbergi* (⅔ natural size). B. *Protosuchus richardsoni*, after Walker (1970) (⅔ natural size).

RELATIONSHIP OF THE PROTOSUCHIANS TO FORMS OF QUESTIONABLE CROCODILIAN AFFINITY

In 1967 Sill suggested *Proterochampsa barrionuevoi*, of late Middle Triassic age from South America, as the most ancient of known crocodilians. Sill believed that *Proterochampsa* is closely related to *Notochampsa*, and that *Protosuchus* is representative of a more aberrant line of crocodilian heritage.

According to Sill, in both *Notochampsa* and *Proterochampsa* the skull is relatively long compared to width, is flat, and the orbits lie in the horizontal plane. There is, however, no reason at all for supposing that the orbits of *Notochampsa* are dorsally orientated as Sill claimed. On the contrary, it seems much more likely that they face laterally as in *Orthosuchus*. Again, Sill relied heavily on Haughton's description (1924) of the auditory region of *Notochampsa*, and claimed that a further resemblance to *Proterochampsa* could be found in the

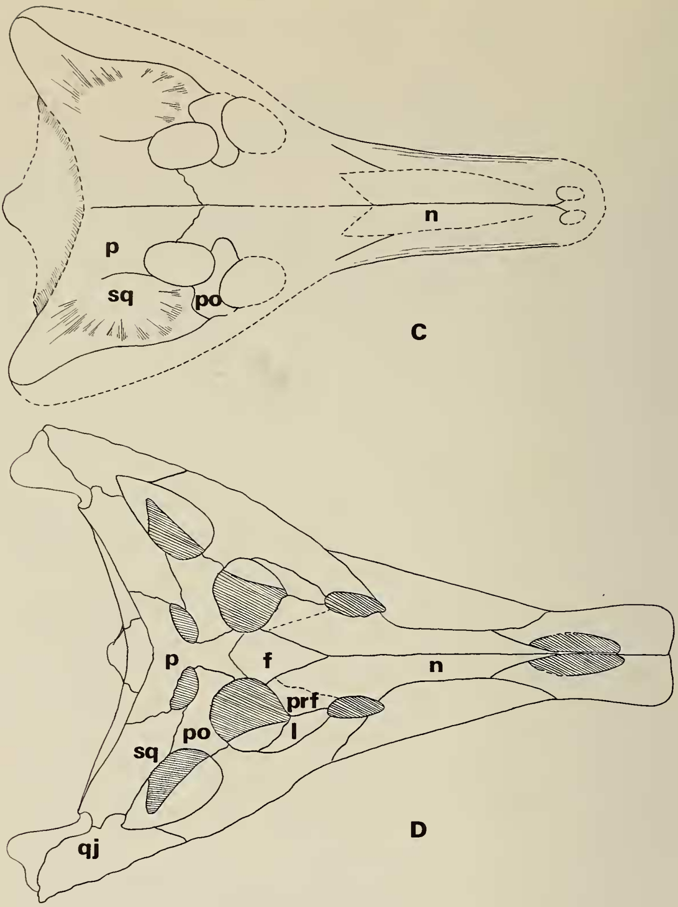

Fig 44 *continued* C. *Notochampsa istedana*, after Broom (1927) ($\frac{2}{3}$ natural size). D. *Proterochampsa barrionuevoi*, after Sill (1967) ($\frac{2}{9}$ natural size).

presence of an auditory canal on the posterior face of the skull. However, this description of the type specimen of *Notochampsa* cannot be correct; the skull of specimen British Museum (Natural History) No. R8503 shows a deep otic recess, and pronounced otic notch.

The resemblances between *Notochampsa* and *Proterochampsa* are clearly not impressive, whereas the similarity between the skulls of *Orthosuchus*, *Protosuchus* and *Notochampsa* is striking (Fig. 44). Sill (1968 personal communication) now agrees that he cannot substantiate his earlier claims, though he doubts the phytosaurian affinity of *Proterochampsa* postulated by Walker (1968). In Walker's view (1970) the position of the choanae alone is sufficient to exclude *Proterochampsa* as a crocodilian ancestor.

The vertebral column of *Proterochampsa* is known only from the thirteen most anterior vertebrae. Rather surprisingly, the parapophysis retains a low position on the centrum throughout this series. Presumably it changes position farther back along the column, and so may parallel the condition found in some primitive thecodontians like *Chasmatosaurus* and *Erythrosuchus* where the parapophysis does not begin to rise until the eleventh vertebra (Hughes 1963). Indeed, Romer (1971, 1972*a*) has now demonstrated a close relationship between *Proterochampsa*, *Cerritosaurus*, *Gualosuchus* and *Chanaresuchus*. He has argued convincingly that they are a sterile group, representing a modest advance over the Proterosuchia, which in Middle Triassic times occupied a position in the ecology similar to that of the phytosaurs of the late Triassic and the crocodilians of the later Mesozoic.

Stegomosuchus longipes, from the Upper Triassic of the Connecticut Valley, is poorly known because of the form of its preservation. As Walker (1970) has commented, resemblances to protosuchians are seen in the broad, flattened cranial table, in the longitudinal groove which runs along its margin, and in the presence of two supraorbital elements on each side. The skull roof is pitted as in protosuchians. Postcranially, crocodilian affinity is shown by the broad, triangular apex of the scapula, the presence of a calcaneal tuber and four elongated metatarsals of the hind-foot, and the similarity of the dorsal armour. This evidence, though slender, suggests that *Stegomosuchus* may reasonably be regarded as a protosuchian.

Microchampsa scutata from the Upper Triassic of the Yunnan, China, is known only from part of the postcranium. In view of this, Simmons (1965) was hesitant to establish its systematic position but suggested that *Microchampsa* might represent a new type of crocodilian. He described the vertebral structure as most crocodilian, but it is difficult to see what is meant by this, since the pattern found in protosuchians is also common to thecodontians. Further, the neural spines of the posterior dorsal vertebrae of *Microchampsa* are terminally expanded to accommodate the median row of dorsal scutes, and this is certainly not the case in any of the protosuchians. Spine tables are developed on the posterior cervical and anterior dorsal vertebrae of *Euparkeria*, and on the posterior dorsal vertebrae of *Stagonolepis*.

The ribs of *Microchampsa* are also quite different from those of *Protosuchus* and *Orthosuchus*. In *Microchampsa* they are short and entirely devoid of the double flanges so characteristic of protosuchians. Furthermore, in *Microchampsa* the lumbar ribs are fused to lateral scutes; an impossible condition in protosuchians which lack scutes in this region. The armour, moreover, is not of the type found in protosuchians. In *Microchampsa* there is but a single median row of dorsal scutes, not pitted or ornamented in any way. This row is flanked by a row of dorso-lateral scutes on each side. These are simply pitted and have rugosities. These features, taken together, make a good case for excluding *Microchampsa* from the Crocodilia, and regarding it, for the present, as a pseudosuchian.

The archosaur material from the Upper Triassic of South Wales, at present being studied by Kermack, includes several partly associated skeletons. The skull has an antorbital fenestra, and the carpus is crocodilian in type in that the radiale and ulnare are elongated. With regard to the number of distal carpals present, the specimens from Wales resemble *Protosuchus* and differ from *Orthosuchus.* It is however surprising to find the pelvis and hind-limb more primitive in type than that of both *Orthosuchus* and *Protosuchus.* In Kermack's opinion (1956), the pubis contributes to the formation of the acetabulum, and is perforated by an obturator foramen. It is possible that in *Protosuchus* the pubis contributes marginally to the acetabulum, but in neither *Protosuchus* nor *Orthosuchus* is it perforated. On the other hand the acetabulum is open, and the ischium similar in each case.

Kermack described the metatarsus of his material as having a fifth digit with two reduced phalanges, and likened it to the metatarsus of *Erythrochampsa.* However he relied upon Von Huene's interpretation of *Erythrochampsa* which is now shown to be incorrect. In view of the crocodilian nature of the pelvis, and also of the carpus, there is little doubt that the Welsh form is a primitive crocodilian, differing in a number of respects from the South African and North American forms.

Hemiprotosuchus leali, from the Upper Triassic of Argentina, is represented by a skull and jaws, and several postcranial elements. Bonaparte (1971) believes it to be a protosuchian, and has closely compared *Hemiprotosuchus* with *Protosuchus.*

Hemiprotosuchus is of moderate size, much the same as other known protosuchians. The cranial table has a characteristic crocodilian configuration, though the sculpturing is in the form of rugosities rather than pitting. The interorbital area is slender, as it is in *Orthosuchus*, but the orbit and preorbital region is higher than in other protosuchians. The nares are terminal, as in *Orthosuchus*, and the superior temporal fenestra is elongate, as in *Notochampsa.* An antorbital fenestra is present, as in *Orthosuchus*, and leads to the ventral edge of the orbit.

As is characteristic of crocodilians, the quadratojugal and quadrate are sutured to the postorbital and squamosal in the anterior dorsal region of the inferior temporal fenestra. Further, the squamosal overhangs the otic region which is open posteriorly as in protosuchians. A short, bony secondary palate is developed, and the pterygoid and basisphenoid show the same relationship as found in *Orthosuchus.* The lower jaw is persistently primitive, as in *Orthosuchus* in that a prearticular is present, but a retroarticular process is lacking. However, whereas the jaw in *Hemiprotosuchus* is deep, in *Orthosuchus* it is quite slender.

The characters of the skull indicate that *Hemiprotosuchus* should be regarded as a protosuchian, and the associated postcranial elements confirm this diagnosis. The coracoid is elongated postero-ventrally, the astragalus and calcaneum are crocodilian in type, and the scutes covering the trunk are paired and imbricated. Unfortunately it is not possible to determine whether the scutes are sculptured.

Walker (1970) has suggested that a number of other Upper Triassic genera of disputed affinities are also closely related to, though distinct from, the 'true' crocodiles. These are *Pedeticosaurus* from the Cave Sandstone of South Africa, *Sphenosuchus* from the underlying Red Beds, *Hesperosuchus* from the Chinle Formation of Arizona, *Saltoposuchus* from the Stubensandstein of Germany and *Platyognathus* from the Dark Red Beds of the Lower Lufeng Series, Yunnan, China.

Bonaparte (1971) has since demonstrated that the skull of *Pseudhesperosuchus jachaleri* is closely similar to that of *Sphenosuchus acutus.* He is of the opinion that rather more significance should be placed on differences between the skulls of sphenosuchians and protosuchians, notably the absence in sphenosuchians of the typical crocodilian cranial table, and the pseudosuchian nature of the basicranium, suspensory region and palate. Hence, although sphenosuchians are transitional between thecodontians and crocodilians, in Bonaparte's view they show a series of characters which relate them most closely to thecodontians.

Bonaparte has further suggested that *Pseudhesperosuchus* is closely linked to *Hesperosuchus agilis.* Evidence for this is based mainly on the form of the coracoid and humerus. Bonaparte and Walker are both of the opinion that the 'problematical' element figured by Colbert (1952) is a coracoid, and there can be little dispute about this identification. However, according to Colbert, this element consists of two bones sutured together, the suture being interrupted by a large foramen. In my opinion this element resembles a therapsid coracoid rather than that of an archosaur. Colbert had, in addition, identified the proximal portion of the left coracoid of *Hesperosuchus.*

Should the 'problematical' element prove to be the coracoid of a different animal, and not that of *Hesperosuchus,* then the latter shows no crocodilian characteristics. In *Sphenosuchus* the coracoid is elongate, and in *Pseudhesperosuchus* the coracoid, radiale and ulnare are all elongated, but the presence of certain diverse crocodilian features in these types does not in itself confirm crocodilian affinity.

Pedeticosaurus leviseuri (Van Hoepen 1915) is preserved mainly as an impression of the right side of the skull and limbs. The skull, as far as can be seen, differs little from that of known protosuchians. The scapula, humerus, radius and ulna appear to be similar in general outline to these elements in *Orthosuchus,* though the coracoid is unknown. Walker has suggested that the element previously identified by Van Hoepen as a metacarpal is an elongated radiale associated with the first metacarpal and two phalanges. This could indicate crocodilian affinity, but since no other bones of the carpus and manus are present, this cannot be confirmed. Although the evidence is slight, on balance it seems that *Pedeticosaurus* lies closer to protosuchians than to forms like *Sphenosuchus.*

Saltoposuchus is at present too inadequately known for a meaningful comparison to be made.

Platyognathus hsui represents an unusual type in that the teeth are irregularly polygonal, and finely denticulate. The jaw also differs from that of protosuchians in that it is short and terminally expansive. The development of a rudimentary secondary palate in this type was regarded by Simmons (1965) as a crocodilian characteristic, but this type of development has also been noted in such diverse forms as *Sphenosuchus*, *Erpetosuchus* and phytosaurs. It does not compare with the form of the palate in *Orthosuchus*.

Simmons (1965) described the vertebral column of *Platyognathus* as being protosuchian, but with procoelous centra. The latter is clearly a very remarkable character in a form of Upper Triassic age, and is found in neither thecodontians nor protosuchians. The vertebrae also differ from those of protosuchians in the development of spine tables. Further, the dorsal ribs show the unusual condition of being flanged on the sternal segment. The dorsal scutes are paired and overlapping, but bear rugosities as well as pits. Indeed, the only crocodilian character present is seen in the elongate form of the coracoid. This is clearly insufficient reason to link *Platyognathus* with the Protosuchia, and its affinities more probably lie with the Pseudosuchia.

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ABBREVIATIONS

a	angular	m	maxilla
af	antorbital fenestra	n	nasal
ar	articular	p	parietal
bo	basioccipital	pa	prearticular
bpt	basipterygoid process	pl	palatine
bs	basisphenoid	pm	premaxilla
c	coronoid	pmf	premaxillary foramen
ch	choana	po	postorbital
con	condyle	popr	paroccipital process
d	dentary	prf	prefrontal
ec	ectopterygoid (transverse)	pt	pterygoid
en	external naris	q	quadrate
eo	exoccipital	qj	quadratojugal
eu	median opening of eustachian tubes	s	stapes
eul	lateral eustachian pit	sa	surangular
f	frontal	so	supraorbital
fch	position of functional choana	soc	supraoccipital
ic	foramen for internal carotid	sp	splenial
gl	jaw articulation (glenoid fossa)	sq	squamosal
itf	inferior temporal fenestra	stf	superior temporal fenestra
j	jugal	tm	tympanic membrane
l	lachrymal	v	vomer
ls	laterosphenoid		

A.M.N.H.	American Museum of Natural History, New York
B.M.N.H.	British Museum (Natural History), London
S.A.M.	South African Museum, Cape Town
Zool. Mus.	Zoologisches Museum, Berlin

Foramina for cranial nerves in roman numerals